

[*Miss Frances Pitt*]

PINK-FOOTED GEESE IN FLIGHT

BIRD MIGRATION

A Short Account

By

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" And fainter onward, like wild birds that change
Their season in the night, and wail their way
From cloud to cloud, down the long wind the dream
Shrill'd; but in going mingled with dim cries
Far in the moonlit haze among the hills."

Tennyson, " The Passing of Arthur."

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MADE IN GREAT BRITAIN.

PREFACE

THE first edition of this book was written in response to a request for a short account of bird migration, in simple terms: the present edition has been revised and brought up to date. The scope of the work is broadly indicated by the titles of its four main divisions: Introduction to Migration; Some Aspects of Migration; General Features of Migration; and Theories about Migration. The main treatment has been kept as general as possible, but in the choice of detailed examples the standpoint of readers situated in Great Britain and Ireland has been allowed to predominate.

Those who wish a fuller statement are referred to the author's earlier and larger *Problems of Bird-Migration* (1926), which aimed at a scientific presentation of the subject. That work is supplemented, as regards subsequent additions to knowledge, by a paper which he published (1936) in the *Ibis*, the journal of the British Ornithologists' Union, under the title "Recent Progress in the Study of Bird-Migration: a Review of the Literature, 1926-35"; and more recently by abstracts which he has contributed to the magazine *British Birds*.

The existence of these other works has relieved the author on this occasion from the necessity of giving evidence in support of every statement, of citing authorities except where these are specifically quoted, or of discussing many views which are not accepted. Nor does he attempt here to enter into details such as are of interest chiefly to the technical ornithologist or the general biologist.

The author's thanks are due to all those, named elsewhere, who have permitted the use of illustrations; and to his wife for much help at every stage in the preparation of the book.

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CHAPTER I

THE STUDY OF MIGRATION

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Historical Sketch

FROM very early times the coming and going of different birds with the changing seasons has been remarked by mankind. Some knowledge of migration must have formed part of the lore of early man before the dawn of history, as it does among primitive peoples at this day. In ancient literature there are many references, and poets of our own time have also made frequent allusion.

In the *Iliad* the Trojan army is likened to a horde of cranes, fleeing the wintry storms and steering their course across the sea with dissonant clamour. The question is asked in the *Book of Job*: "Doth the hawk fly by thy wisdom and stretch her wings toward the south?" In the *Book of Jeremiah* we read: "Yea, the stork in the heaven knoweth her appointed times; and the turtle and the crane and the swallow observe the time of their coming." In the works of Aristotle the subject is discussed with considerable understanding, although views which we now know to be erroneous are also entertained. In medieval times various fantastic theories were widely accepted. It was thought, for instance, that

swallows passed the winter lying dormant in the mud at the bottom of lakes and ponds, and that cuckoos turned into hawks until next spring, while some seriously held that birds journeyed to the moon. Belief in hibernation persisted, even among the literate, well into the eighteenth century. Probably, indeed, it lingers even to-day as a superstition: colour is given to it by the way in which swallows congregate in the reed-beds before their autumnal departure, and by the occasional finding of dead or moribund birds in such situations.

Scientific Investigation

In our own time the migration of birds has become a subject of scientific investigation. It is of concern not only to ornithologists and bird lovers, but is of much interest to general biologists as an outstanding example of animal behaviour. It appeals to the imagination, also, as one of the great natural phenomena, dramatic in its manifestations and charged with the wonder of life.

The study has likewise some practical value with regard to the protection of migratory birds which are of economic importance, whether as game or in relation to the control of insects harmful to agriculture. It is for this latter reason that investigations into migration receive government support in some countries, as instanced by the work of the Hungarian Institute of Ornithology at Budapest and by the U.S. Bureau of Biological Survey at Washington. In North America the protection of migratory birds is the subject of an effective treaty between Canada and the United States, with particular reference to wildfowl considered to be valuable as game. In Europe, the movement for international conventions on bird protection has to contend with political

difficulties and differences in viewpoint that make concerted action harder to achieve. It is worth noting, however, that even within the United Kingdom the question of migration is relevant to measures of protection which differ as between one local area and another.

A great mass of authentic information is now available, but our knowledge is still very far from complete. Difficulties of observation prevent the ascertainment of essential facts, without which it is impossible to fill gaps in the picture. On the theoretical side, important advances have been made in our understanding of the question: there nevertheless remain many points that we are unable to explain, and problems to which no certain solution can yet be offered. In the following pages the attempt is made to present, in broad outline, the main facts of migration as now known, and those explanatory theories to which some credence can be given.

Methods of Study: Observational

Before proceeding with the subject itself, it will be useful to consider the sources of modern knowledge regarding it, and the means by which this is being increased. Methods for the study of bird-migration are, generally speaking, of three kinds. In the first place, there are direct observational methods, which necessarily deal with movements of birds in the mass. Then there is the marking method, whereby individual birds are brought under investigation. Finally, there are possibilities of experiment, in which trial is made of various deliberate changes in the conditions affecting particular birds.

Observation depends largely upon opportunity.

In an ordinary inland district it is not easy to note more than the periodical disappearances and reappearances of different species: only rarely is a movement seen in progress. On the coast, it is often possible to witness the actual arrivals or departures. At favoured stations, notably islands lying in the path of important migrations, the passage of birds may sometimes be seen on a grand scale, and there can be few more impressive sights than a great diurnal " rush " in which tens of thousands of birds stream past within a few hours. At other times, an index to unseen flights may be given by the birds which are each day found resting on a small island: a restricted area with few resident birds, and no other land very near, is of obvious advantage to the observer. When conditions are suitable, nocturnal movements may be seen at lighthouses or on lightships, the birds being especially attracted to the dazzling beams in misty weather.

The classic example of a migration observatory is the island of Heligoland, in the south-eastern corner of the North Sea. This was made famous towards the end of last century by the life-long observations of Heinrich Gätke. His work gave a great impetus to the study, although in some of his statements, and especially in his speculative assumptions, his enthusiasm sometimes outran his judgment. His work has since been resumed by others on the lines of modern scientific inquiry. The Germans had meanwhile established another station at Rossitten; this is not on an island, but on a narrow isthmus separating a great lagoon from the sea at the south-eastern corner of the Baltic.

The British island which is best known in this connection is Fair Isle, lying midway between the Orkney and Shetland groups. It was the most

fruitful of those on which periods of observation were spent by Dr. Eagle Clarke, and it has since yielded many remarkable records. Much work has also been done on the Isle of May, in the Firth of Forth, and on Skokholm, off the coast of Pembrokeshire. Many other places in different parts of the world have proved to be vantage points for the study of migration.

Concerted schemes for the collection of observations made simultaneously at many different points are especially valuable. The collection of records from lightkeepers, over a period of years, was organized by a committee of the British Association in "the eighties" of last century. The results, as worked out by Dr. Eagle Clarke, form the basis of our knowledge of the movements affecting the British area. They have been supplemented, notably, by a collection of observations not restricted to light-stations or even to the coasts, under the auspices of the British Ornithologists' Club. Similar work has been done in other countries—with especial success in Hungary and by the late Professor Wells Cooke in the United States of America.

Bird-Ringing

In bird-marking, as we have said, the individual is singled out. The method consists of marking large numbers of birds with light aluminium rings, stamped with an address for reply and a serial number for identification. Naturally, only a few of these birds are heard of again, but the exact information which the records yield as to the journeys performed by these individuals gives them great value. Birds are ringed either as chicks unable to fly, or as adults caught in traps or by other means. Except where birds return to the traps, as very

frequently happens, the subsequent records depend mainly on chance.

No doubt many ringed birds are shot, captured or found dead by persons who have not sufficient interest or public spirit to report the occurrence: still more will not be seen at all. Apart from recoveries at the place of marking, most small birds yield only about one per cent. or less of records. Larger birds, such as plovers and gulls, may give from two to five per cent. Birds which are commonly shot for sport are reported in larger proportion, up to twenty per cent. or more in the case of some ducks. The figures are naturally subject to great variation as between one country and another, according to the conditions which favour reporting, and this fact has always to be borne in mind in any attempt at statistical analysis.

Very early cases are on record of the marking of odd birds in some primitive way. The first attempt worthy of particular mention, however, is that of Lord William Percy, who in 1890 began marking young woodcock in Northumberland with rings inscribed with "N" and the year: some interesting records were secured in spite of the poor chances of getting returns from a distance. The first scheme for marking different kinds of birds, using rings with an adequate address and identification numbers, was that instituted by Mortensen in Denmark in 1899. A few years later, work on a large scale was taken up in Germany and in Hungary. In 1909, ringing schemes were launched in Great Britain by Mr. H. F. Witherby, in connection with the magazine *British Birds*, and by the present writer from the University of Aberdeen. The former still continues, and was transferred in 1937 to the control of a special committee of the British Trust



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RINGING A CHAFFINCH



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BRITISH BIRD-MARKING RINGS

for Ornithology: the headquarters are at the British Museum (Natural History), and the rings now bear that address. (The scheme can claim a total of nearly three-quarters of a million birds ringed, and the results are freely quoted in the following pages). Important ringing work has also been done in Holland and Sweden, especially, and there are schemes of varying magnitude in many other European countries, and in Egypt, India and Japan. In North America, after some earlier beginnings in a smaller way, ringing ("banding") has been done on an enormous scale since 1920 with the official support of the U. S. Biological Survey.

In recent years, particularly in America, there has been a great development of systematic trapping as an aid to ringing. This has opened up many new lines of inquiry, not all of which have to do with migration. The harmlessness of the method is shown by the readiness with which most birds—of the kinds commonly caught—acquire "the trap habit", returning again and again with the greatest persistence. The regular operation of a trap at a given spot thus enables a bird community to be kept under close observation, with proper control over the identification of individuals. Information has in this way been obtained regarding the period of stay in a locality, the persistence of group associations, and the regularity of return in subsequent seasons. Evidence as to actual journeys depends in any event upon chance records from a distance, and for this purpose the ringing of young birds before they can fly is in general the most useful method: the results are more easily interpreted when the place of ringing is known to be the bird's native locality, whereas the origin of a bird marked in other circumstances is usually a matter of doubt. Nevertheless, much has

been learnt as the result of ringing birds trapped during actual migration at places such as Heligoland.

Experimental Methods

One type of experimental approach to the problems of migration consists merely in removing birds from their proper localities, either to test their homing powers or to ascertain how they migrate from a different place. In such work, and in other studies involving intensive observation of a small group of birds, the usual numbered rings are often supplemented by marks of identification visible on the bird at liberty—coloured celluloid rings on the feet or patches of dye on the plumage. In experimental work with captive birds, the effect is tried of artificially altering various conditions which seem likely to influence behaviour, as exhibited either in the aviary or on subsequent release.

Migrations of Other Animals

To see our special subject in true perspective, it is necessary to notice that migration in some form is characteristic of many kinds of animals. Some of the cases are most remarkable, but no more can be done here than to mention a few examples very briefly.

Some periodical movements involve drastic changes in the nature of the habitat without a journey of any great length. Thus, among crustaceans, the land-crabs of some tropical islands have become mainly terrestrial in their habits, but remain dependent on the sea for reproduction and early development. At the appropriate seasons mass movements take place between one habitat and the other. A converse case is found among reptiles:

turtles spend most of their time at sea, but must resort regularly to the beach to lay their eggs.

Other movements involve the performance of extensive journeys. Many insects are notable travellers. This is proverbial in the case of locusts, which at irregular intervals invade new territory in enormous numbers and with destructive results to all vegetation in their path. These flights are sustained movements of dense swarms of insects proceeding in a definite direction. Butterflies of many kinds are migratory in high degree, some performing regular seasonal movements in which huge numbers may take part. There are, for instance, several species which do not survive the winter in the British Isles, but which appear there annually as immigrants. Definite return movements seem to be the exception rather than the rule.

Among fishes, many purely marine species perform seasonal movements of considerable extent. Owing to the economic importance of this question, much research has been done on the subject: a method of marking individual fish is largely used. The salmon provides an instance of migration between salt water and fresh. The adult fish feeds and grows in the sea but comes up the rivers to breed: there the young pass through the first stages of their development before going down to the sea.

In contrast, we have the very remarkable case of the eels which reproduce in the oceanic depths but grow to maturity in fresh water. Eels of the species which visit European rivers are hatched in the abyss of the North Atlantic, rise to the surface as transparent larvæ, make for the coast, and go up-river as "elvers" with the dimensions of knitting needles. After some years the full-grown fish return to the ocean to breed and are no more seen. Eels of another

species are bred in the same ocean but make their way to the rivers of eastern North America.

Among marine mammals, whales of various kinds perform extensive movements. These are being investigated, by marking and other methods, for economic reasons. Some species of seal also travel great distances, returning to breed on shore at particular places.

Some terrestrial mammals change their ground with the seasons. Thus, in Newfoundland there is a regular southward migration of caribou on the approach of winter. In parts of Africa, great movements of game animals take place in avoidance of periodic drought. Some kinds of bats migrate—the fruit-bats of Australia, for example. There are also less frequent movements, such as those of the Norwegian lemming. Every few years the numbers of this small rodent increase to such an extent that the animals overflow their usual area in the mountains and invade the lower levels in great hordes. Nothing turns them from their course: rivers are crossed despite heavy losses, and often the procession reaches the sea and heads out towards inevitable destruction.

It is not wholly irrelevant to mention the movements of the highest animal of all, man himself, without going so far as to consider those deliberate journeys which are made for one reason or another under the conditions of civilization. There are still at this day races of mankind, following a primitive manner of life, which exhibit a nomadic state such as was probably characteristic of an early phase in human evolution. Hunting peoples naturally tend to follow the game upon which they depend, moving as the animals change their ground. Pastoral peoples travel with their flocks and herds as the seasonal

influences on vegetation may demand. Even under civilization this latter motive for periodic change of habitat persists to some extent, and in mountain regions we commonly find a kind of "vertical migration" between a winter home in the valleys and a summer home on the high pastures.

As regards animal migrations in general, three main types of movements may perhaps be distinguished. Firstly, there are regular to and fro journeys related to seasonal conditions—of which the scarcity or abundance of food is probably the most important. Secondly, there is regular resort to a particular habitat which satisfies special requirements of reproduction. These two types are often combined. Thirdly, there are less regular movements, commonly without any return counterpart, which have the appearance of efforts at range expansion.

It may be noted that in many cases the migration is repeated annually by the same individuals, but that in some—the eel, for instance—it occurs only once in each lifetime. Some of the irregular movements occur at such intervals that whole generations of individuals pass purely sedentary lives. On the other hand, in the case of short-lived insects, a single movement may be continued by successive generations, each wave making a further advance.

We may now return to our particular subject, and see what types of movement are found among birds.

CHAPTER II

DIFFERENT TYPES OF MIGRATION

Local movements—Dispersals and wanderings—Typical migration—Trans-equatorial migration—Oceanic migration—Migration within the tropics—Irregular movements.

MANY kinds of migratory movements are found among birds. These movements vary, as between one species and another, not only in their geographical extent, but also in the degree to which they are definite and regular. A rigid classification is not possible, as every gradation between different kinds of movement can be found; nor would it help our purpose. It will be useful, however, to distinguish a few main types of movement, and to consider representative examples of these by way of illustrating our general theme.

Local Movements

In the first place, there are birds which perform merely local movements of a seasonal character, such as may seem scarcely worthy to be called migrations. These movements may consist of nothing more than a change of ground for the winter, associated with the different manner of life at that time of year. During the summer many species are restricted to particular localities which happen to satisfy the special requirements of their breeding habits. When they cease to be so tied, they become free to spread more evenly over the countryside in search of food. In other cases the change of ground may be in a definite direction, as for instance from an inland

district towards the more open conditions of the adjacent coast.

Other local movements may be rather longer, but still performed entirely within the particular geographical area. Many examples could be quoted of species found in the British Isles of which the native individuals perform migrations that do not extend beyond the limits of the country. The starling is a case in point. The results of ringing have shown that, although the birds native to other countries are migratory in greater degree, those breeding here keep within our shores. Autumn journeys are made southwards and westwards within Great Britain—for instance, from Stirling to Cheshire or from Hampshire to Cornwall, while other birds cross from Scotland and northern England to Ireland. Only one case is on record of a marked native starling quitting our shores, and that bird merely crossed from Kent to the opposite side of the English Channel.

A special kind of local movement may perhaps be described as "vertical migration". It occurs in mountainous regions, and consists mainly in a seasonal change of level. In an extreme case this may involve descent from the hilltops to a very different environment in the valley thousands of feet below, but without a journey of any great distance as measured horizontally on the map. On this point Dr. Wetmore[1] writes: "Wherever large mountain ranges are found in temperate regions we find regular migration taking place up and down their slopes. Such migration may be noted in India, where bird migrants from Siberia mingle on the plains with others that have merely descended the near-by Himalayas."

[1] A. Wetmore (1926). *The Migrations of Birds.* Cambridge, M[illegible]

A good example of a vertical movement is given in the show-case illustrating bird-migration in the British Museum (Natural History). This is the white-capped redstart of the eastern Himalayas. It breeds on the mountains at elevations of between about 7,000 and 13,000 feet above sea-level. In winter it descends to the adjacent foothills, and its altitudinal range at that season is approximately from 2,000 to 8,000 feet.

Dispersals and Wanderings

We may next consider journeys which are more extensive than a local movement, but nevertheless still lack the regular character of a true migration. These are rather indefinite wanderings in which the breeding-place is the only fixed point, and which extend over a wide area during the autumn and winter. The implication in the term "dispersal" is that of outward spread from a centre: this should, ideally, take place evenly in all directions, in so far as these may be considered open to birds having the special needs of the species concerned. Very often, as it happens, a dispersal shows a definite bias in some particular direction.

Dispersals are especially characteristic of some sea-birds which are concentrated in vast numbers at certain places during the breeding season, but during the rest of the year are scattered over a wide area of sea. They may go in all directions—that is, for marine species, in all seaward directions—or they may favour some special quarter. The guillemot, which breeds in colonies on cliff-bound sections of our coastline, provides an example of this kind of movement. The facts have been brought out by the results of ringing: guillemots of known British origin have in this way been traced, during the win-

ter months, northwards to the Faeroe Islands, eastwards to southern Norway and Sweden, and southwards to the west coast of France and the north coast of Spain. Much ringing of this species has also been done on Heligoland, where guillemots bulk largely among the few breeding birds. Many of these remain during the winter in the neighbouring waters of the south-eastern region of the North Sea, but others spread to great distances. In the early winter months especially, very many are found further north, round the southern coasts of Norway. Others go westwards and southwards, through the English Channel to the Bay of Biscay, while still others penetrate into the Baltic Sea.

For comparison we may take another sea-bird, the gannet, which shows a very distinct southward tendency in its winter wanderings. This great bird breeds at only a few stations in the world, and particularly in a number of large colonies on islands off the British coasts. Of the birds which have been ringed there, some have been recorded further north or further east than the British Isles. In the great majority of cases showing journeys of any length, however, the recovery localities lie southward along the Atlantic coasts of France, Spain, Portugal, Morocco, and West Africa—to within ten degrees of the equator. Thus, several gannets ringed as chicks on Grassholm off the Pembrokeshire coast, or on the Bass Rock in the Firth of Forth, have been recovered off the Rio de Oro in mid-winter when they were about six months old.

It may be a matter of some difficulty to distinguish between a dispersal, especially one with a directional trend, and a definite migration. The essential point in a dispersal is that the concentration of individuals remains greatest near the point of origin, and that

their numbers become progressively less as the distance outwards increases. In a migration there is a shift in what may be called the centre of gravity of the population.

The distinction may be brought out by comparing the movements of two closely allied species of similar habits, both native to the British Isles, the herring-gull and the lesser black-backed gull. Young birds of each of these species have been ringed in fairly large numbers, and an analysis of the resulting records can be used to supplement the distributional evidence. The herring-gull is common throughout the year, so it is only by ringing that anything definite can be learnt about the movements performed. If the numbers of recovery records are plotted according to the distance from the place of marking, date and direction being ignored, a typical dispersion curve results: the number of records falls in each successive zone of two hundred miles, and reaches zero at 600-800 miles. The lesser black-backed gull, on the other hand, is obviously a migrant, as it becomes quite scarce in winter. A curve of its records, constructed in a similar manner, falls still more steeply at first, approaches zero, and then rises to a second peak at 1,000-1,200 miles: moreover, a map of the record localities clearly shows the southward direction of the movement. The significant point is not that the birds of one species travel further than those of the other, as happens to be the case, but that the distribution of the true migrant becomes centred round a different point in winter than in summer.

Typical Migration

When we come to typical migration, however, the difference between it and any kind of mere dispersal

is quite obvious. By "typical migration" we mean movements developed to a considerable pitch of regularity, definite in their directions and important in their extent. There is in it more than a seasonal drift of the bird population towards some particular quarter. There is, in fact, a real abandonment of the area of summer distribution, in favour of a different area that serves for winter habitation. The relation between these two areas may vary from case to case, in ways which we shall notice presently.

Almost any species of bird which is commonly thought of as a migrant will serve as an example, and those which are known as summer visitors to the British Isles come most readily to mind. In this group we have, for instance, such different birds as the swallow, the nightingale, and various warblers; the cuckoo and the swift; the turtle dove, the common sandpiper, and several species of tern. All of them are well known to us as breeding birds, but are entirely absent from the country in winter.

To consider one case in more detail, the nightingale breeds in Europe, roughly speaking, from the shores of the North Sea to those of the Mediterranean. In the British Isles its range is restricted, and it is really common only in the south and south-eastern parts of England. Outside Europe, the summer distribution extends to adjacent portions of Asia and also includes north-west Africa. In winter, on the other hand, the nightingale is an inhabitant of tropical parts of Africa, north of the great equatorial forests.

North America will supply an example just as easily. For instance, the scarlet tanager is a native of the north-eastern United States and of adjoining parts of Canada. This region is occupied only in summer, and in winter the species is found in the

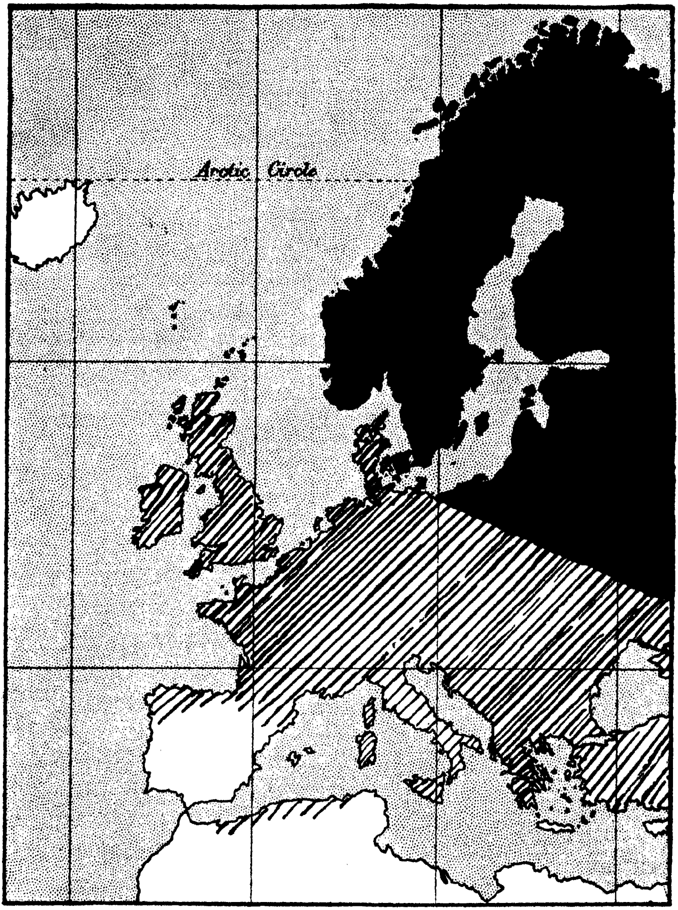


FIG. 1.—BREEDING AREA (black) AND WINTERING AREA (diagonals) OF THE FIELDFARE

Mainly after an exhibit in the British Museum (Natural History)

An example of a hardy migrant, wintering in the temperate zone. The two areas adjoin, and even overlap to some extent. Compare the swallow (Fig. 2).

north-western countries of South America—Columbia, Ecuador, and Peru—astride the equator.

Or, again, take one of those species which are known to us as winter visitors, although much less familiar to most people than the summer birds. Thus the fieldfare, a species of thrush, is a native of northern and north-eastern Europe and Asia. In winter it is found in central and much of southern Europe, and also in the western countries. During the summer it is common in Scandinavia, but in the British Isles it is known only as a winter visitor, from October to April. A somewhat similar case is that of the snow-bunting, if we ignore the fact that a few pairs remain with us in the summer to breed on Scottish mountain-tops. This species has a wide summer distribution in sub-arctic lands, and seeks more temperate latitudes for the winter: those that visit us probably come from Iceland, and even Greenland, as well as from Scandinavia.

It should be noted that the distinction between "summer visitors" and "winter visitors" is a matter of local point of view, and that these do not necessarily represent different types of migratory movement. The fieldfare is a winter visitor in the eyes of the British observer, but is known as a summer visitor to the inhabitants of Norway. The nightingale is a summer visitor with us, but it is a winter visitor to most of northern Africa.

As already mentioned, the geographical relation between the summer area and the winter area of a species may differ considerably between one case and another. Sometimes the two areas are quite separate, and even widely distant from each other. The species is then purely a summer visitor in the one and purely a winter visitor in the other: in the intervening region it will be known merely as a bird of passage,

appearing temporarily twice a year at the seasons of migration. In other cases the two areas may be close together and may even overlap. In the latter event there will be an intermediate region where the species is to be found all the year round, although it is purely a summer visitor further north and purely a winter visitor further south: it does not follow, however, that any of the birds in the permanently inhabited area are actually sedentary, as a complete seasonal replacement of individuals may conceivably take place.

In the extreme case of overlapping areas, the winter range is wholly within the summer range. What happens is that in winter the species becomes concentrated in the more southerly part of the region over which it is distributed; the individual birds native to that part are practically resident therein, while the others are migratory. We have already noticed, for example, how the starlings native to the British Isles are resident, except for the local movements within the country which some of them perform. But in winter the starling population is greatly increased by the presence of birds which have come as visitors from parts of the Continent subject to more severe conditions at that time of year.

Notwithstanding what has been said above, it would be a mistake to suppose that exactly the same type of migration is exemplified by a British summer visitor such as the nightingale and a British winter visitor such as the fieldfare. They are classed in that way on a purely local basis, as we have seen, but there is another difference between them of a more general kind. Consideration of the seasonal distribution of the nightingale, already indicated, shows that it breeds in the summer of the north temperate zone, but that in autumn it withdraws into the

tropics; in other words, it avoids winter altogether. The fieldfare, on the other hand, remains within the temperate region and does no more than seek a rather milder climate for the winter.

This may perhaps seem to be a difference merely of degree, but in reality its significance is greater than that. The one bird gets completely away from the influence of the seasonal changes characteristic of higher latitudes. The other remains within the sphere of the northern winter, although experiencing its conditions in a less severe form than if it had not migrated at all. Species that come within this second group are sometimes classed as "hardy migrants", to distinguish them from those which retire to the sub-tropics or further.

Transequatorial Migration

The extreme case of the typical migrant is the real long-distance traveller which does not stop even in the tropics, but changes its habitat from the northern temperate or arctic zone to the southern temperate zone. This is of course a very remarkable phenomenon, whether regarded as an actual performance or from a theoretical standpoint. The result is that these trans-equatorial migrants have "no winter in their year". They exchange the northern summer for the southern summer, but during the latter they behave as wintering birds—making no attempt to breed, although it is the nesting season for birds of other species which are native there.

The swallow is an example. In our summer it is known throughout almost the whole of Europe, in western parts of Asia, and in north-western Africa. (Allied forms are found in Egypt, parts of Asia, and North America.) In winter it is absent from its

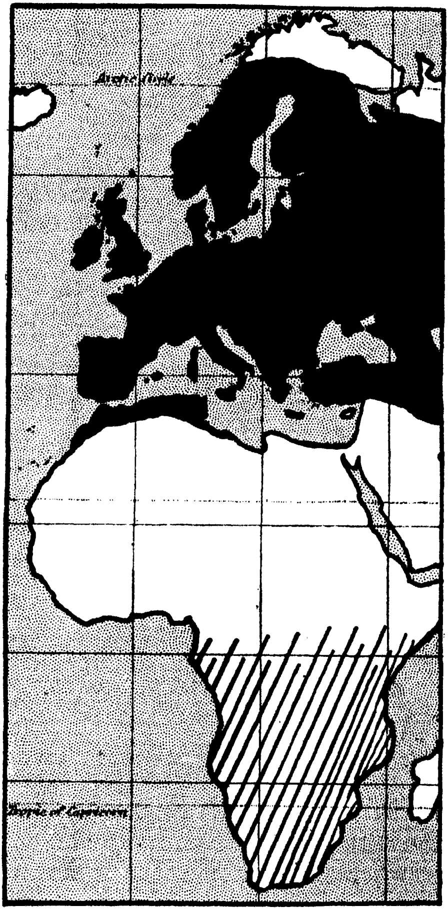


FIG. 2.—BREEDING AREA (black) AND WINTERING AREA (diagonals) OF THE SWALLOW

Mainly after an exhibit in the British Museum (Natural History)

An example of a trans-equatorial migrant. The two areas are far apart, and the "wintering" birds in fact experience a second summer in the Southern Hemisphere. (For ringing records see Fig. 3.)

breeding range except perhaps near the southern boundary, and is found in Africa, as far as the extreme south, and in India. The individuals that reach South Africa find another summer there, as we have just seen. Near Cape Town, for instance, the swallow is first noted at the end of October, becomes common in November, remains till March, and has entirely disappeared by the middle of April.

Fortunately, the results of marking nowadays enable us to say with certainty what some of the journeys are that are performed by individual birds. It has in this way been well established that British native swallows often reach South Africa. It was in December 1912 that a swallow was found near Utrecht, Natal, with a "British Birds" ring, from which it was identified as one that had been marked as an adult at its nest in Staffordshire in June of the preceding year. In the following March another was recovered at Reit Vallei, Orange Free State, which had been ringed as a nestling in Ayrshire eight months previously. Since then there have been well over a dozen records of marked British swallows from eastern South Africa, as well as one from the Congo. It is noteworthy, by contrast, that swallows ringed in Germany have been recovered predominantly in western and central equatorial Africa, with several spring and autumn records from north-west Africa and the Cape Verde Islands. The only record from Egypt is of a bird ringed in Czecho-Slovakia.

The closely related barn swallow of North America is likewise a trans-equatorial migrant. In summer it breeds as far north as Alaska: its winter range extends from Brazil southwards to the Argentine. Other examples will be mentioned in subsequent chapters, in illustration of different points.

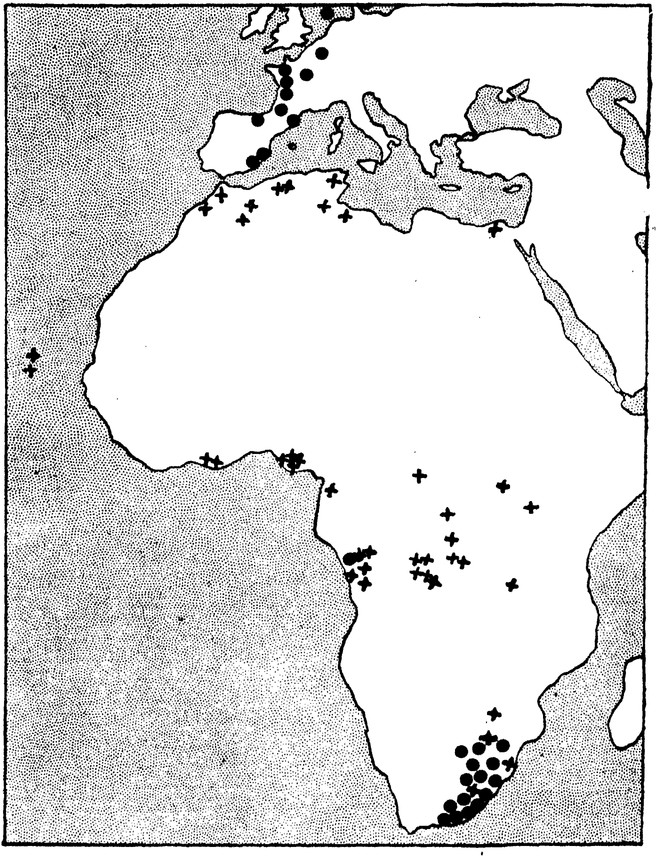


FIG. 3.—RECOVERY LOCALITIES OF RINGED SWALLOWS

Adapted from maps by Witherby and Leach and by E. Schüz

The birds were ringed as nestlings, or in a few cases as breeding adults. Each black spot shows a recovery locality abroad of a swallow ringed in Great Britain. Each cross shows a recovery locality in Africa of a swallow ringed on the continent of Europe. (For seasonal distribution see Fig. 2.)

Among land birds there is no example of the opposite case—a southern species "wintering" in the summer of the northern temperate zone. This fact may be related to the different distribution of the land-masses in the two hemispheres. Most of the long distance migrants are birds which have a breeding distribution extending into high northern latitudes: in the south there is no land in corresponding latitudes, except the isolated continent of Antarctica.

Oceanic Migrations

There are, however, some oceanic birds which breed in the southern hemisphere and migrate across the equator to "winter" in the summer of the northern seas. The great shearwater, a large species of petrel, breeds on Tristan da Cunha and possibly elsewhere in such latitudes. In the northern summer it is common in the North Atlantic and reaches the Arctic Circle. This is no mere random dispersal over a wide area, for the recent work of Mr. Wynne-Edwards[1] has shown that there is a definite movement which quickly passes the tropics.

Among birds native to northern latitudes, the fulmar petrel is common on the North Atlantic throughout the summer, indicating that there are many non-breeding individuals. The numerical distribution in the different months contrasts strongly with that of the great shearwater, the greatest abundance being recorded on the western side of the ocean at the end of the season instead of at its beginning: this suggests the existence of regulating factors other than the richness or poverty of plankton, which is the food of both species alike.

Another oceanic—and also trans-equatorial—

[1] V. C. Wynne-Edwards (1935). In *Proceedings of the Boston Society of Natural History*, Vol. 40, p. 233.

migrant is Wilson's petrel, about which all the available information has been brought together by Dr. Roberts[1]. This species breeds on the rocky coasts and islands of the Antarctic continent, but is absent from there from March or April till November or December, and the migration is described as "one of the longest and perhaps the most remarkable of any bird known". In the Atlantic Ocean, the earliest and largest movement is up the American side, and the dates show that the advance of the vanguard must be rapid. By June the ocean south of the Equator is deserted, and in the height of the northern summer the birds seem to be concentrated towards the two sides of the North Atlantic but most numerously on the western side. The furthest north records are from 52° 30′ N. lat. in American waters and from Jura in the Inner Hebrides. The data from the Pacific and Indian Oceans are less adequate, but the movements extend to the Red Sea and Persian Gulf, to New Guinea, and to northern Peru. In a straight line the Atlantic migration is about 7,000 miles in each direction and the actual distances covered must be much greater.

Migrations of skuas likewise take place far out at sea and may cross wide stretches of ocean. Mr. Brooks[2] has given evidence that the wintering places may be of limited extent, with great concentrations of birds in particular—but often widely separated—waters. Mr. Wynne-Edwards[3] has described a spring migration of long-tailed skuas, or "boat-swain-birds", far out in the North Atlantic: a somewhat dispersed but continuous flock extended as far as the eye could see, countless birds flying low over the water to the northward.

[1] B. Roberts (1940). *In British Graham Land Expedition,* 1934-37 *Scientific Reports,* Vol. 1, p. 141.
[2] A. Brooks (1939). In *Ibis,* XIV Ser., Vol. 3, p. 324.
[3] V. C. Wynne-Edwards (1935). *Loc. cit.*

Migration within the Tropics

We have seen that some migratory movements are confined to the temperate zone, that some extend to the tropics, and that others cross the equator to the opposite hemisphere. It remains to mention that there are also regular migrations which take place wholly within the tropics, on the part of birds which do not come at any time within the influence of alternating summer and winter in the familiar sense. These tropical movements are related instead to the occurrence of wet seasons and dry seasons in different parts: they occur on both sides of the equator, and in many cases cross it. Thus, in Africa, we have Abdim's stork breeding in the northern tropics from May to November, but also widely distributed as a bird of passage in equatorial regions and as a "winter" visitor further south. Another interesting case is that of the broad-billed roller, which breeds only in Madagascar but migrates north-westwards to reach the Congo between June and November. Further examples will be mentioned later.

Irregular Movements

Apart from all the categories of annual movements, there are movements which occur at irregular intervals in the form of invasions or irruptions. The best known example is that of Pallas's sandgrouse. This species normally inhabits the steppes of western central Asia, but in the spring of certain years the birds have "irrupted" in large numbers in a north-westward direction across Europe, reaching the British Isles. They have attempted to breed in the countries they have thus visited, and there is some evidence of a return movement in autumn on the part of survivors. Big invasions occurred in 1863, 1888

and 1900, and smaller ones in other years. Similarly, the rosy pastor—an Asiatic bird related to the starling—makes occasional summer visitations to parts of Europe. Large numbers bred in Hungary as recently as 1908, 1925 and 1932.

A different case is that of the crossbill, which exhibits erratic movements after the breeding season. The latter is variable and often very early, so that the invasions may occur in summer although more commonly in autumn. On such occasions birds from northern Europe visit the British Isles in unusual numbers, and some remain to breed—swelling the small native population—in the following season. From a study of the observations recorded in North America, Mr. Griscom[1] has concluded that the movements are largely governed by food supply, and that they are as likely to take place to the east or west as on a north and south line. In Finland[2], it has been shown that there is a close relation between the number of crossbills inhabiting an area and the abundance of the cone-crop in the spruce forests in the particular year.

There are other birds, such as the waxwing in Europe or the snowy owl in North America, which from time to time perform autumn movements on a scale which is unusual both as regards the numbers taking part and the distances travelled. There are return movements in spring, and the whole would seem to be an exaggeration of the migration which occurs in a normal year. It seems certain that these extraordinary movements are often related to the failure of some staple food supply, such as the berry crop in the case of the waxwing, in the usual winter area; but their cause is obscure, seeing that they sometimes appear to anticipate rather than to follow

[1] L. Griscom (1937). In *Proceedings of the Boston Society of Natural History*, Vol. 41, p. 77.
[2] A. Reinikainen (1937). In *Ornis Fennica*, Vol. 14, p. 55.

the shortage, and to pass quite rapidly through regions of comparative plenty. This is less easy to explain in terms of inherited behaviour than the annually recurring phenomena, but it is to be noted that the species concerned are all migratory to some extent every year.

In the more arid parts of Australia many species seem to be nomadic. Their distribution is subject to change at irregular intervals, as different sections of the country are affected by prolonged drought or by the recurrence of rain after possibly several years. Other birds are said to wander irregularly in relation to the blossoming of the eucalyptus tree, on the flowers of which they feed: in a favourable year for this the musk lorikeet, for example, may be found in great numbers in particular districts.

Some of the regular "hardy migrants" also exhibit what are called "weather movements"—continuations of the autumn migration, or even reversals of the spring migration, apparently as the direct result of specially severe weather occurring late in the winter. The time and extent of these movements vary from year to year according to the nature of the particular season. Other birds, however, are not induced to depart in such circumstances, but perish if conditions pass the limits of tolerance. Similarly, it does not seem that any of the long-distance migrants perform reverse movements in spring, even if late wintry weather occurring after their arrival should threaten fatal results. This has led some writers to distinguish rather sharply between migratory species which they call "weather birds" and those which they call "instinct birds"; but we must be careful not to accept the theoretical implications of the terminology too readily, the ascertained fact being merely that some migrations are more

directly influenced by immediate weather conditions while others tend to conform more closely with a regular pattern.

It may be mentioned that, for the purposes of general discussion in the following pages, irregular movements of the invasion type will not be considered as included in the term " migration ". It is only the annually recurrent phenomena that are regarded as coming within the limits of the strict definition.

CHAPTER III

THE PHENOMENA OF MIGRATION

Appearances and disappearances—Migration in progress: by night—Migration in progress: by day—Flightless migration.

IN the preceding chapter a preliminary account of migration was given, in the form of descriptions of different types of movement which are known to occur. It will be obvious, however, that such an account is possible only as a result of a great accumulation of facts, which is now available in the literature of ornithology through the labours of many observers all over the world, and through the use of different methods of inquiry. First-hand knowledge of migration must at best be a very fragmentary thing, however great one's possibilities of travel and of study.

What, then, are the actual phenomena of migration—the happenings which the single observer may hope to see? These will of course depend very greatly upon his opportunities, and also upon his good fortune. Let us therefore consider what these may be.

Appearances and Disappearances

We have already mentioned that little or nothing of actual migration is to be seen in an ordinary inland district. The observer is aware only of the seasonal appearances and disappearances of some species, and perhaps of changes in the abundance of others. Even a naturalist of the calibre of Gilbert White, at a time when people were still obsessed

by ideas of hibernation, had nothing more than this kind of circumstantial evidence as regards the Hampshire parish of Selborne which he knew so well. "We must not, I think, deny migration in general: because migration certainly subsists in some places, as my brother in Andalusia has fully informed me. Of the motions of these birds he has ocular demonstration."[1]

Nevertheless, although he cannot unaided gain much impression of migration as a whole, the local observer may find great interest in filling in the details of his particular corner of the general picture. His task is naturally easiest with those species which are altogether absent during some part of the year—birds which are purely summer visitors or purely winter visitors to his country, or at least to his district. In these cases he can record in successive years the first appearance of each species, its increase towards normal numbers, and the date on which it was last seen. For some other birds, never wholly absent, he may possibly be able to detect evidence of migration in seasonal fluctuations in their abundance. The presence of a sewage farm, or of a reservoir or small lake, greatly adds to the opportunities, as such places are temporarily used by passing migrants of species not ordinarily present in the district. If he participates in a ringing scheme he will have occasional news of the travels of individual birds from his locality, or of their reappearance there or in some neighbouring district in subsequent years. When ringing is combined with systematic trapping, he will have a section of his bird population under close study.

In a coastal district other opportunities may be added. Actual arrivals or departures over the sea may be witnessed, or flights following the line of

[1] Letter to Daines Barrington, 1771.

the coast. The seashore and river estuaries, too, are often the resort of flocks of birds—such as sandpipers of various species—resting and feeding for a while at an intermediate stage in their migration.

Most favourable of all, certainly, is a small island, if it lie in the path of important movements. Unless too near other land, such a place will tend to great concentration of resting migrants within a limited area which can be kept under close observation. Probably, also, the permanent bird population will be negligible, so that almost every bird seen may be put down as a migrant, and every record of a species not present on the previous inspection will imply a movement of some kind. As already mentioned, Heligoland is the classic example of an island observatory for the study of migration. Scarcely less famous, however, is Fair Isle, midway between Orkney and Shetland.

The great advantages of Fair Isle have been thus described by their discoverer, Dr. Eagle Clarke[1]: "The outstanding feature of its bird-life is the importance of the passage movements, for the observation of which it is not only unrivalled as a British station, but has few equals anywhere. Extraordinary numbers of these migrants appear regularly during the spring, when on their way to, and in the autumn when returning from, their wide and far-extending nesting-grounds in Northern Europe, Iceland, and Western Siberia. The knowledge gained from the Fair Isle statistics has thrown a flood of light upon these important, and in some respects obscure, migrations, such as was never before possessed for the British Islands. It has been ascertained with a surprising degree of accuracy what species participate regularly in these great movements, and the dates

[1] W. Eagle Clarke (1912). *Studies in Bird Migration*. London (Vol. II).

between which they are performed at both seasons. It has been possible, also, to note the increase in the stream of migrants under incentives highly favourable for their performance, its arrest during stressful periods, or, again, its even flow under ordinary conditions: in other words, the island has afforded the opportunity of correlating the diverse movements with the weather conditions, and ascertaining what the meteorological incentives, checks, and barriers, as the case may be, to migration are—a knowledge of the relations existing between the two sets of phenomena which was highly desirable."

Migration in Progress: by Night

Even in the relatively favourable circumstances of a coastal station or small island, so much migration takes place by night that little of its actual performance is visible. Sometimes, however, it may be clearly heard, and even in the great cities the cries of birds passing overhead on a still night will occasionally reveal the presence of the travellers. Under better conditions the sounds may indeed give evidence that a great movement is occurring.

As Dr. Wetmore[1] has said: "Records of nocturnal flight are made easily by the ear, as many birds call during these flights by night. During the rush at the height of migration these notes, coming constantly from the darkness, produce a profound effect upon the imagination. Calls come from near and far, some of them easily recognized, and some so distant or so mingled with others that they are indistinct. At times there may be a medley in which half a dozen species may join, or again a band of some particular form may pass with their cries coming from all points of the air, to the exclusion of others. The impression given at times is so vivid

[1] A. Wetmore (1926). *Op. cit.*



[L. S. V. Venables]

PART OF FAIR ISLE

Famous stopping-place of migrants

that instinctively one strains the eyes against the darkness in a vain attempt to pick out the migrant whose vibrant calls come from so near at hand that the birds seem almost within reach."

On clear nights migrants may sometimes be seen as they fly across the face of the moon, but it is really only at lighthouses and lightships that nocturnal migration becomes visible to any extent. In certain weather conditions the nocturnal flights present a wonderful spectacle at the lantern, when the migrants are attracted by the beam: it is only white lights that have this effect, and lanterns which have been altered to give a coloured beam have been found to cease attracting the birds. An experience at the lighthouse on the Isle of May in the Firth of Forth has been well described by Miss Rintoul and Miss Baxter.[1]

"On May 9th, 1911, with a light south-east wind and small rain, we watched on the balcony of the lighthouse, from midnight to 3 a.m., a big rush of willow warblers, wheatears, greater wheatears, whinchats, redstarts, goldcrests, and meadow pipits. This was a very beautiful sight, the birds not being so strongly attracted by the light as to dash themselves against the glass, merely fluttered up to the lantern and remained gazing in, fascinated by its powerful rays. At this time the light had four flashes, and the four long rays of light shone out into the darkness, turning all to gold which came within their beams. The drops of rain looked golden, the birds coming up the rays appeared golden, and, to add to all this wonderful beauty, as they fluttered up the rays some of them sang soft little snatches of song. At the first hint of dawn the

[1] L. J. Rintoul and E. V. Baxter (1935). *A Vertebrate Fauna of Forth*, Edinburgh.

birds ceased coming to the light, and in ten minutes the rush to the lantern was over. As soon as it was light enough, we went out to see what was on the island, and found huge numbers of these and other birds everywhere."

Migration in Progress: By Day

Although so much migration is nocturnal, many species travel habitually by day and others sometimes. On almost any coast or island large diurnal movements may occasionally be witnessed, and in some places they are of regular occurrence. There can be few sights in nature more impressive than a really great diurnal migration under good conditions of observation. The maximum effect, constituting a so-called "rush", is sometimes produced by a sudden change in the weather after a period when migration has been temporarily suspended at the height of the season. Again from the Isle of May, for instance, the same writers as before give us an account of a great passage, chiefly of thrushes of different kinds, on October 6th, 1926. "In the early hours of the morning we were awakened by the fog-horn going on; we listened, but could not hear any sound of migrants. About three hours later we were again awakened, this time by the horn going off, and immediately became aware that an enormous movement of birds was going on in the darkness. There were continual notes of migrants, the 'zieh' of the redwing, the 'zip' of the thrush, the chuckle of the fieldfare and ring ouzel—alike and yet so distinctive—all combined to show that numbers of species as well as individuals were on the move. We tried to see as much as we could in the rays of light, always a difficult and unsatisfactory method of identification, but found the birds were not coming

up close to the lantern, so waited with impatience for dawn. As soon as there was even an apology of daylight out we went, and found the island swarming with birds. No words can describe the multitudes: redwings were the most plentiful species, the island was thick with them, great flocks were coming in from the north-east, lighting on the island for a few minutes and then passing on to the south-west. Innumerable flocks passed over the island in the same line without stopping; looking up into the sky we could see them flock above flock as far as the eye could reach. In addition to this huge number of redwings there was a big passage of fieldfares. They came in large flocks, and we noticed that the passage of the redwings ceased before that of the fieldfares, as the end of the movement was composed largely of the latter species. Continental song thrushes and blackbirds (mostly young males) were in great abundance."

The greatest manifestation of migration that the present author has witnessed was on the coast near Rossitten, at the south-eastern angle of the Baltic Sea, the site of the well-known German ornithological station. That is a place where immense diurnal movements are regularly seen, at the proper season: in the particular year it was on October 2nd that they first attained a considerable scale. Picture a sandy shore stretching unbroken as far as the eye could see, north-eastward towards Russia and south-westward toward the Gulf of Danzig. On one side lay the quiet waters of the almost tideless sea; on the other rose a line of low dunes over which the tops of the trees behind peeped here and there. The silence was complete but for the rhythmic murmur of gentle waves; a slight breeze blew from the south-east, and the sky was lightly clouded at a great height, leav-

ing the lower air extremely clear. The sun shone brighlty, but the keen nip of October was in the air, showing that despite the glorious weather the autumn had entered on its final phase and winter was at hand. The steady progress of the crow battalions told the same tale. Every minute or two a flock passed, flying steadily and quietly south-westward along the line of the shore at a height of from 100 to 300 feet. Hooded crows were in the majority, rooks, numerous, and jackdaws present in smaller numbers; rooks and crows were generally in separate flocks, the jackdaws accompanying the former. If one watched a flock pass overhead and recede in the distance, another was already passing before it had disappeared, and a third would be coming into view in the wake of the second. The line of the shore seemed to be followed with some exactness, for a bend a quarter of a mile away caused the flocks to fly out over the sea for a few hundred yards before they wheeled to take the slightly altered direction. In size the flocks varied from thirty or forty to two or three hundred birds; and we calculated that over two thousand birds passed every hour in an unbroken stream from early morning till after midday.

Next day was as beautiful as its predecessor, and the number of migrants greater than ever. Crows there were, as on the day before; but the flocks were larger and more frequent, and continued to pass till well on in the afternoon. Some twenty or thirty thousand must have passed in the course of the day. It was not merely the vastness of the numbers that made the scene so impressive, but the fact that all these thousands were moving together with one accord, without great speed or appearance of haste, yet without halt or deviation and still more noticeably without noise. The great army was advancing in



[*R. M. Lockley*]

ISLE OF MAY: THE BIRD TRAP

Used in catching migrants for marking and release.

column—a column of great length but of no appreciable frontage, and apparently without any parallel columns in its near neighbourhood. Not only was there a continual succession of these silent flocks of hooded crows, rooks, and jackdaws, but small song-birds were also on the move. Every few seconds a small company of larks or a little band of finches passed us flying low down over the ground. Overhead, at a considerable altitude, were less frequent flocks of woodpigeons, making more speed than most of the others. Here and there were a few birds of prey; kestrels were frequent, usually alone, sometimes three or four together; and often, at one's approach, some larger predatory bird would rise on broad wings from a meal provided by some weakling which had paid too high a price for the journey.

For another impression we may quote the description by Admiral Lynes[1] of an incident in the autumn migration of storks in the eastern Mediterranean. "During September, 1906, H.M.S. *Scylla* was at anchor off Alexandretta, in the Gulf of Iskanderun, at the very north-east corner of the Levant. For an hour or so during the forenoon (from memory I think it was about 10.30 to 11.30), for several days in succession, there was a considerable stream past the ship of white storks, about eight or ten every hundred yards, steering a dead straight south-easterly course. They appeared to be flying in rather a leisurely way, between ten and fifty feet above the surface of the water, and were obviously just crossing, by the shortest route, the mouth of the gulf, a distance across the water of some twenty-five miles. On reaching the far shore of the gulf (our side), they stayed their progress a little to assemble, wheeling around and mounting higher and higher, about five

[1] H. Lynes (1909). In *British Birds*, Vol. 3, p. 36.

thousand strong—an impressive spectacle. Gradually they drew away, still circling round and still apparently rising, until finally, perhaps half an hour after the last of the pack had passed the ship, the whole concourse of storks became lost to view at an immense height over the hills in the direction of Aleppo."

For another example we may seek the very different conditions of eastern Greenland, from where Mr. Spencer Chapman[1] has thus described an autumn rush of departing sea-birds: "On October 10th we saw a most unusual sight. There was no wind, but low cloud, mist and falling snow restricted the visibility to about half a mile. Out by Ailsa the sea was suddenly alive with birds. Whereas formerly we had seen only one or two Brünnich's guillemots a day, here we saw literally hundreds. Flock after flock of little auks were going south, either flying or swimming in their jerky way upon the water. We saw more black guillemots in an hour than we had seen during the rest of the autumn. Owing to the poor visibility it was impossible to estimate the numbers of migrating birds. The day before we had seen only the usual number, and two days later the Brünnich's guillemots and little auks had passed on; only a few black guillemots remained."

How apparent the facts of migration are in some parts of the world is shown by this quotation from the works of Hudson[2] relating to the Argentine. "I can almost say that when I first opened my eyes it was to the light of heaven and to the phenomenon of bird-migration—and the sight and sound of it. For migration was then and there on a great, a tremendous scale and forced itself on the attention

[1] F. Spencer Chapman (1934). *Watkins' Last Expedition*, London.
[2] W. H. Hudson (1922). *A Hind in Richmond Park*, London.

of everyone. The autumnal migration, which was always a more impressive spectacle than that of the spring, began in February, when the weather was still hot, and continued for three long months; for after the departure of all our own birds, the South Patagonian species that wintered with us, or passed on their way to districts further north, would begin to come in. During all these three long months the sight and sound of passage birds was a thing of every day, of every hour, so long as the light lasted, and after dark from time to time the cries of the high travellers came to us from the sky."

Flightless Migration

There are migrations which involve no flight. Penguins of various species, although unable to fly, perform regular seasonal movements of some extent. The winter area of some of them is in the region of the floating floes of pack-ice some hundreds of miles north of the nesting grounds on the land of the Antarctic continent. The greater part of the journey is made by swimming, but on their arrival off their native coasts in spring there may still be some miles of unbroken sea-ice between open water and solid ground. This has to be traversed on foot, and at the height of the movement the birds coming to a particular colony may form an unending line of thousands of individuals.

The arrival of penguins at the South Orkneys was thus described by Dr. Rudmose Brown of the Scottish Antactic Expedition of 1902-4[1]: "The great event in the spring was undoubtedly the return of the penguins to their rookeries. That signified surroundings full of life, a never-failing

[1] R. N. Rudmose Brown, R. C. Mossman, and J. H. Harvey Pirie (1906). *The Voyage of the 'Scotia'*, Edinburgh.

field of interest to naturalists, and last, though almost most important, a plentiful supply of eggs and fresh meat. In the second week of October they began to arrive in large numbers from the north, all of the black-throated kind, and in a few days' time the large rookery at Point Martin was filled with a noisy excited crowd of birds busying themselves in settling down for nesting. The birds came in large flocks, all moving determinedly for their chosen rookery, often in their hurry adopting their prone mode of progression—propelling themselves forward on their bellies by aid of feet and flippers. In that fashion they are able to travel over the floe considerably faster than a man on skis can follow them, as we often had reason to learn when we were bent on a penguin hunt."

Nor is it necessarily only flightless birds that migrate otherwise than through the air. Sea-birds such as the guillemot, although well able to fly, probably make the greater part of their journeys by gradual progress on and under the water. There are also pedestrian movements. A land migration of American coots has been described, in which large numbers travelled northwards on foot in the Warner Valley, Oregon, in May. They did not swim, but followed the water's edge, walking from six to twenty-five abreast, and it was estimated that at least ten thousand passed in four days. Bean geese in full moult have also been described as travelling on foot across the Siberian tundra.

PART II
SOME ASPECTS OF MIGRATION

CHAPTER IV

THE DIRECTIONS OF MIGRATION

Direction in relation to climate—Migrations of European birds—General trends: Old World—General trends: New World—Transoceanic migration—Movements in the British area—Migration routes.

Direction in Relation to Climate

IT is usual to think of migration as being from north to south, and *vice versa*. For the purposes of general discussion it is convenient to accept these directions as normal, but in fact this is far from being a universal rule. There are of course many places where the distribution of land does not permit of due north and south migration. In addition, however, there is much migration that diverges widely from the longitudinal line without any such reason. It is even common for migration to take place between regions lying east and west of each other in practically the same latitude.

A more general rule is that autumn migration, following the breeding season, is from an area having a relatively severe winter to an area having a milder climate at that time. Migration is indeed adapted to climatic conditions, and it is well known that these depend on many other things than latitude alone. The axiom is that every bird breeds in the coldest part of its range, but even to this there are some exceptions.

One of the other factors which determine climate is altitude, and we have already noticed examples of what may be called vertical migration between different levels in mountainous regions. Of wider importance is the great difference which is often to be found between the climate in the interior of a continental mass and in its coastal regions. The effects of ocean currents on the climate of different coasts is also a factor.

Migrations of European Birds

These questions have great significance for bird migration in western Europe. In this region a milder winter climate is to be found on the western seaboard and islands, as well as towards the south. Much migration, accordingly, proceeds in autumn in a south-westerly direction, and some of it actually from east to west. The general trend of a large part of the migration from Scandinavia is south-westerly towards Great Britain, France and Spain. From the Netherlands, northern Germany and the Baltic countries much of the migration in autumn is almost due westwards towards Great Britain, much of the rest being south-westwards. Even from Hungary, whence the natural outlet would seem to lie elsewhere, many birds travel westwards to southern France and south-westwards to Spain and north-west Africa.

These facts have long been known, both from the seasonal distribution of various migratory species and from the direct observation of migration in progress at different points. More recently they have been firmly established by numerous records showing what journeys are performed by individual marked birds. We have already noticed that the starlings native to the British Isles are no more than local migrants within the country, but that in winter

their numbers are increased by an influx of visitors bred abroad. The immigration is on a great scale and is frequently observed; the ringing records help to fill in the details of the picture.

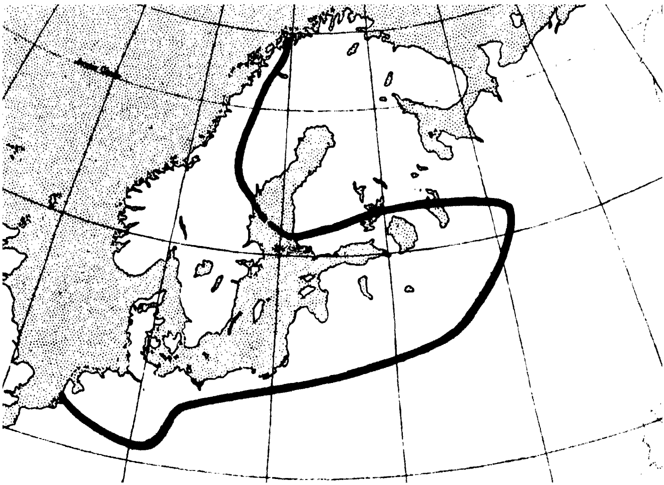


FIG. 4.—NATIVE AREA OF STARLINGS VISITING THE BRITISH ISLES. IN WINTER

Based on data of Witherby and Leach

The area circumscribed by the black line and by the continental seaboard is that within which starlings ringed in Great Britain in winter have been subsequently recovered during the breeding season. These records are now too numerous to show separately, and there are many further records of starlings marked with foreign rings in the breeding season at various places in the same area and recovered in winter in the British Isles.

The earliest record of the kind was one of a starling trapped and marked with an "Aberdeen University" ring near Edinburgh in March 1911, and reported in the Norwegian district of Salten,

just above the Arctic Circle, in the following month. Since then there have been many records of starlings ringed in Great Britain as winter visitors, and recovered in their summer quarters in Scandinavia, Finland, Russia, Holland, and northern Germany. There are also records in the opposite direction—starlings ringed in these continental countries in summer and recovered here in winter. From central European countries, journeys of starlings south-westwards to France, Spain, Italy, and north-west Africa have similarly been shown.

For most birds that are summer visitors to the British Isles, the direction of autumn migration is approximately southwards, through western France, Spain and Portugal. Any great westward divergence is prevented by the Atlantic Ocean, and only a few species show much tendency to travel south-eastwards. The only five records of cuckoos marked in Great Britain and recovered on the Continent are from eastern France, Belgium, Germany and northern Italy (two): there is another from the Cameroons. Similarly, the only two British wood-warblers so far recovered abroad were reported from southern Italy. These two species, however, are exceptional in this respect.

On the continent of Europe a south-easterly direction is favoured, notably, by the white storks native to Denmark, northern and eastern Germany, and Hungary: those bred in western Germany, and some also from Denmark, proceed in the south-westerly direction which is usual for most other species. These facts have been ascertained by the ringing of large numbers of young birds in the easterly migration is indicated on the map by recovery records in the Balkan countries, in Asia countries named. The general course of the south-

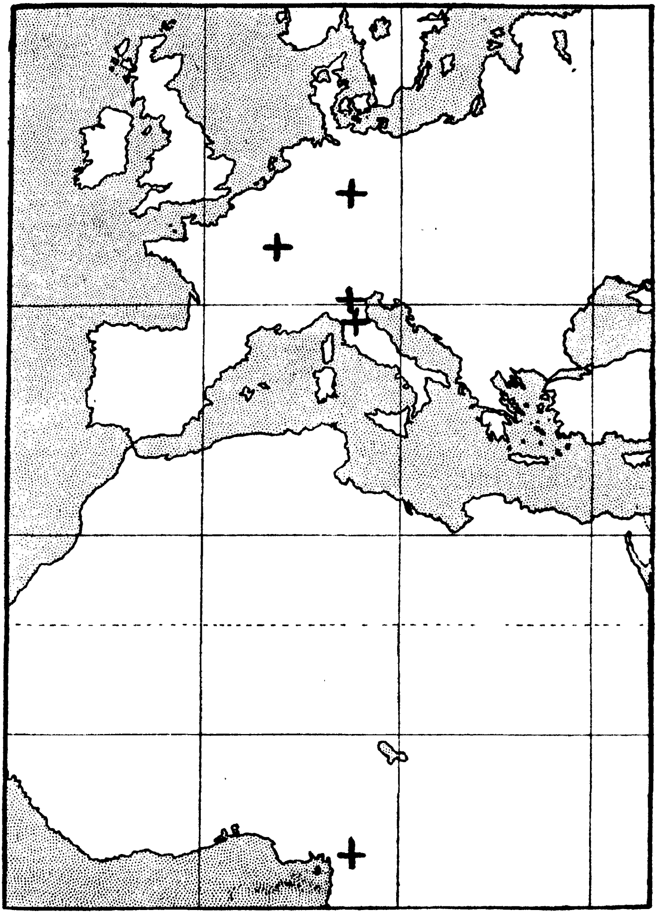


FIG. 5.- RECOVERY LOCALITIES ABROAD OF CUCKOOS RINGED IN GREAT BRITAIN

After Witherby and Leach

The birds were ringed as nestlings, and each cross indicates a recovery; there has been a record from Belgium, in addition, since the map was made. The records so far obtained suggest a more south-easterly course across Europe than is usual for most species native to the British Isles. Compare the European recoveries of British swallows (Fig. 3).

Minor, in Syria and Palestine, in Egypt and the Sudan—and so down through the tropics on the eastern side of the continent to winter quarters in South Africa. There is also a record of a Hungarian stork from south-eastern Arabia, and one of a German stork from Northern India, in its first winter, showing that a few take a still more easterly course. There are some records from parts of Africa lying west of what appears to be the commonest route: at least in part, these probably relate to birds that have travelled south-westwards through Europe.

Another species which shows a south-easterly trend in its autumnal departure from Europe is the red-backed shrike. Observational evidence on this point is confirmed by results of ringing in Germany [1], the recovery records being from eastern Mediterranean countries and East Africa.

In the extreme east of Europe we find examples of southward migration to Egypt. Mr. Mackintosh [2] has reported, for instance, that quail ringed in the latter country in winter have been recovered on passage in Syria and the Balkans, and in a breeding area in southern Russia between the Dnieper and the Volga.

General Trends: Old World

In Europe, then, we may say that the general trend of migration in autumn is to the west and the south, towards the Atlantic seaboard and the Mediterranean, and that a south-westerly direction is especially characteristic. A smaller amount of migration takes place towards the south-east, and some of this extends into Asia. For most of the

[1] H. Ecke (1936). In *Vogelzug*, Vol. 9, p. 123.
[2] D. R. Mackintosh (1941). In *Bulletin of the Zoological Society of Egypt*, No. 3, p. 7.

migrants that go beyond the confines of Europe, however, the winter quarters are in northern or tropical Africa. In the case of the most extensive journeys, South Africa is reached.

We may note, also, that Europe itself provides winter quarters for some of the hardier migrants which come southwards from Greenland or westwards from parts of Asia. In the North Atlantic, too, there may be found during the northern summer certain sea-birds native to the Southern Hemisphere.

Less is known about migration in Asia. It is nevertheless certain that there are autumn movements westwards or south-westwards into Europe, as already mentioned, and eastwards or south-eastwards to the parts bordering on the Pacific Ocean. There is also very much migration into the southern peninsulas and islands of the continent, particularly India and Ceylon on the one hand, and Malaya, Indo-China and the East Indies on the other. Most of the evidence relating to these movements is based on study of the seasonal distribution of various species, and is not yet to any extent amplified by records of journeys performed by individual marked birds. Some ducks of different kinds, notably wigeon, have nevertheless been ringed in India during the winter and subsequently recorded in Siberia during the breeding season.

There are also Asiatic birds which leave that continent, some of them for Australasia and some of them for East Africa. An important stream of migration, for instance, passes from Persia and Iraq to Abyssinia and the Sudan: further north, many birds from the north-east also reach Sinai and Egypt. We have already seen that Asia receives some winter visitors from Europe: a few also come from Alaska across the narrow seas.

Africa not only provides winter quarters for many European and Asiatic birds, but it is also the scene of movements on the part of species confined to that continent. The purely African migrants are of two kinds. In the first place there are the birds which are summer visitors to the southern temperate zone, breeding in South Africa: these move north towards the equator during the southern winter. There are said to be over thirty species which have this status in South Africa, including no less than nine kinds of cuckoo. In the second place there are the birds which are confined to the tropical belt, but nevertheless migrate from one region to another within it. Their movements are not related to summer and winter in the ordinary sense, but to an alternation between a wet season and a dry season.

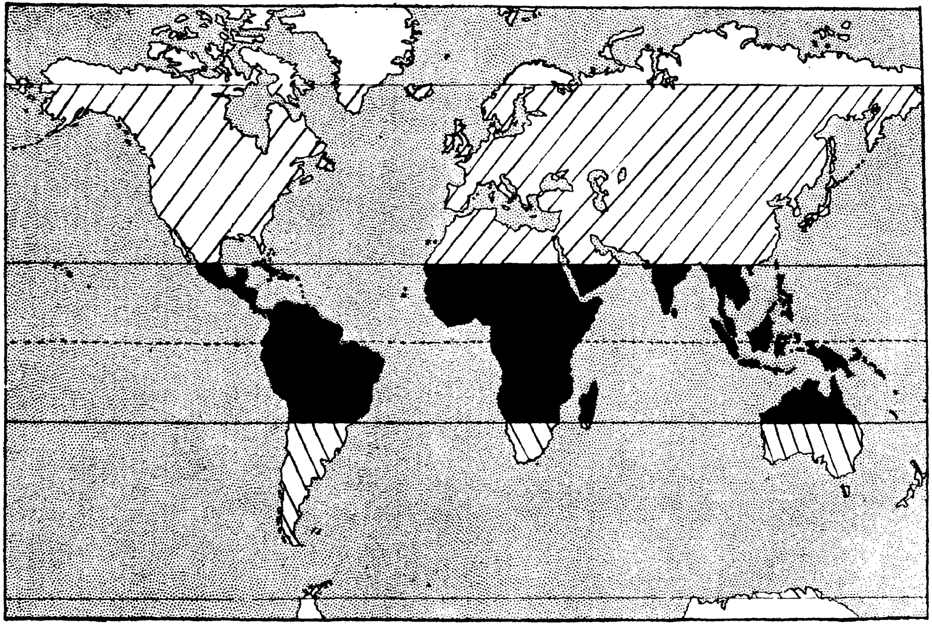
Australasia receives some Asiatic birds as visitors at the time of year which is winter in the Northern Hemisphere. Those which "winter" in Australia include a few true land birds, such as the needle-tailed swift and the Pacific swift, but those reaching New Zealand are all either sea-fowl or else shore-birds of the plover family.

Among native Australian birds, a few are summer visitors to the southern parts—including Tasmania—and withdraw towards the tropical north for the winter. These include the species which has been significantly named the welcome swallow. Little is known about migration in Australia, however, owing to the absence of observers over a large part of the continent. Many birds appear to be nomadic rather than truly migratory, as we have already seen, changing their area in a rather irregular fashion in adaptation to a climate in which whole regions may suffer unbroken drought for several years.

New Zealand has two native land birds which are

. 6.—DISTRIBU-
ON OF LAND IN
IE TROPICAL
lack), TEMPERATE
iagonals), AND
CTIC (white)
ZONES

Mercator's Projection



summer visitors to the islands, and as such, particularly worthy of notice in view of the remarkable nature of the journeys involved. The long-tailed cuckoo finds winter quarters in some of the Polynesian islands, including Fiji and Samoa, and the bronze cuckoo in the Solomon and Bismark groups.

General Trends: New World

Migration is well developed in North America, as might be expected from the climatic extremes to which much of the continent is subject, and it has been extensively studied there. The general position is comparable with that in Europe, if we include part of northern Africa with the latter. There are birds which move southwards within the continent on the approach of winter: the main directions of movement seem to be more directly north and south than in Europe, probably owing to the shape of the land mass, although there is some deflection of migration eastwards and westwards towards the respective coasts. There are also birds which are only summer visitors to North America: these winter in Central America, the West Indies, or South America. In the extreme case they cross the equator and find "winter quarters" in the southern temperate zone, while it is summer there.

For instance, the rose-breasted grosbeak breeds in the north-eastern United States and southern Canada, and winters in Central America and the north-western corner of South America. The bobolink (or rice-bird), native to the same general region, crosses the equator to the southern tropics in Brazil and Paraguay. The upland plover (or Bartram's sandpiper), which has a breeding range extending north to Alaska, comes south to the Argentine.

The migration of North American birds to winter quarters south of that continent follows a number of different main directions, of which the general trend is necessarily southwards or south-eastwards. On the western side, a continuous coastal or overland route by way of Central America is the most direct. From the centre and the east many birds either coast round or cross over the Gulf of Mexico to Central America. On the east, other birds fly from Florida, by way of Cuba and across the Caribbean Sea, direct to South America, while still others keep further east along the great curve of the Antilles. Finally, a few birds make an oceanic crossing direct from Nova Scotia to the Lesser Antilles and thus to South America.

It seems to be the case that South America provides winter quarters for northern birds to a lesser extent than Africa. It has no northern sub-tropical zone, such as accommodates many migrants in northern Africa, and it is also possible that the tropical forest belt offers a greater barrier than in Africa to the passage of trans-equatorial migrants. As we have just seen, there are nevertheless many North American birds which visit the southern continent, some of them reaching the extreme south. Of movements among purely tropical birds in South America little is yet known.

In the temperate region of southern South America there is much migration on the part of birds which breed there and move north towards the equator for the winter. In the Argentine, as in the British Isles, there are thus summer visitors and winter visitors: the summer birds breed there and then go north for the winter, when their place is taken by other birds which have bred in colder regions further south. There are also present in summer a few species from

North America, "wintering" in the Southern Hemisphere.

Transoceanic Migration

We have discussed migration in the Old World and in the New as if they were quite separate, although analogous. In the main they are, as the existence of the wide oceans between would lead us to expect, but there are some exceptions of much interest.

It has already been mentioned that there is some movement between the continents in the north, where these come closer together: some Alaskan birds migrate to Asia, and some Greenland birds to Europe. From Iceland migration takes place both south-eastwards to Europe and south-westwards to North America. For instance, among the ducks breeding on that island, the wigeon has been shown to migrate partly in the one direction and partly in the other: birds marked there with Danish rings have been recovered in the British Isles and other parts of Europe, and also in Newfoundland and on the east coast of Canada and the United States.

The wider oceans are also crossed, although with regularity only in the case of sea-birds. Several birds marked in Europe have been recovered in North America. These include black-headed gulls and kittiwakes. The latter case is specially remarkable in that transoceanic records form about half the total. Of kittiwakes ringed as nestlings in the British Isles, five have been recovered in Newfoundland, one in Labrador, one in southern Greenland, and one in Davis Strait west of Greenland. A kittiwake from the Murmansk region of Russia has also been reported from Newfoundland. Two black-headed gulls marked in Germany have crossed the

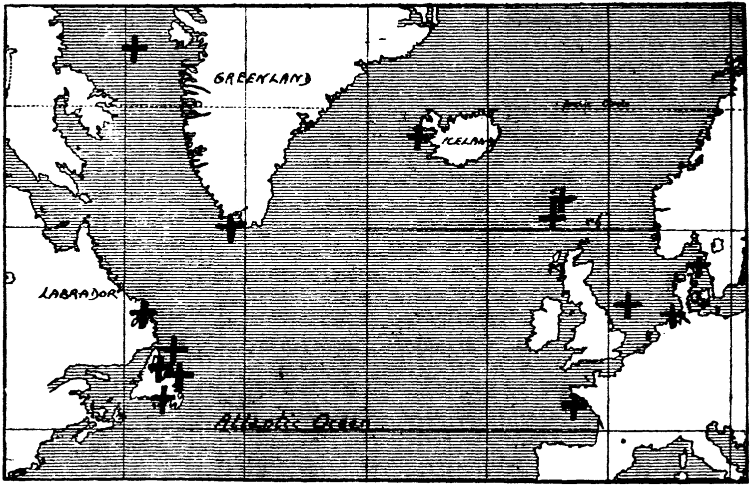


FIG. 7.—RECOVERY LOCALITIES ABROAD OF KITTIWAKE GULLS RINGED IN THE BRITISH ISLES

After E. P. Leach

Each cross shows the recovery locality abroad of a kittiwake ringed as a nestling in the British Isles: there has been a fifth record from Newfoundland since the map was made. The proportion of trans-oceanic records is remarkable.

Atlantic, one to Mexico and the other to the Barbados, but in this case there are very many other records to show that journeys of quite moderate length are more normal.

A great skua ringed in the Shetland Islands has been recovered on the east coast of the United States in its first winter; and there are two records of puffins ringed in the British Isles reaching Newfoundland. A Caspian tern from Lake Michigan has been recorded in Yorkshire, but as this was a summer record after an interval of twelve years it does not necessarily indicate a direct crossing in northern latitudes. There is, in addition, a Barbados record of a gull-billed tern marked in Denmark, and various ringed birds have found their way as far as the Azores: these latter include a spoonbill and a heron from Holland, a black-headed gull from Great Britain, and a scoter from Iceland.

Among land birds, examples of various purely Old World species from Europe are occasionally reported in North America, although cases of this kind may be regarded as accidental. A good instance is that of the lapwing, which occurs only as a rarity in America: as will be mentioned again, a large flock reached Newfoundland in December 1927, and subsequently parts of the mainland; it included a marked bird of British origin.

There is also observational evidence, supported by a few ringing records, to show that arctic terns bred on the eastern side of North America commonly cross the Atlantic to the coasts of Europe and Africa. Individuals of not a few purely North American species reach Europe from time to time as vagrants. In the other direction, the Pacific golden plover is a regular migrant from Alaska to the Hawaian Islands in the middle of the ocean, involv-

ing a very remarkable flight of which more will be said.

The ocean wanderings of various sea-birds in different parts of the world may also be mentioned. Some kinds of petrel, especially, cover very great distances and pass from one ocean to another. The nearest winter quarters for the sea-fowl which breed on the coasts of the Antarctic continent—except those which, like the penguins, can remain at sea—are obviously in South America, South Africa, and Australasia.

Movements in the British Area

Having completed a general survey of the main trends of migration throughout the world, we may now turn to a more detailed consideration of the movements which occur in a particular area, namely the British Isles.

Beginning with autumn migration, we have to do with four principal movements, although these overlap both in time and in space, and also as regards the species taking part. Firstly, there are local movements of native birds within the British Isles, including migration from Great Britain to Ireland and dispersal of various aquatic birds over the surrounding seas. Secondly, there is the departure of native birds which are only summer visitors to this country. Thirdly, there is the arrival of winter visitors from abroad. Fourthly, there is the passage of birds for which our area represents only an intermediate stage between their summer quarters and their winter quarters.

The immigration of winter visitors and passage migrants takes place from several directions. From the north and northwest come birds from Greenland, Iceland and the Faeroe Islands. This movement

strikes our north-western and northern seaboard, including the Shetland Islands. From the north-east come birds from Scandinavia and beyond—Spitzbergen, northern Russia, northern Siberia. This movement strikes the eastern side of Great Britain, especially between Shetland and the Humber estuary. From the east come birds from Holland, Denmark, northern Germany, the Baltic States, and Russia, with others from northern Europe by the same route. This movement strikes principally those parts of England which lie immediately north and south of the Thames estuary, from the Wash to the Straits of Dover. Subsequent passage movements of birds which arrive from these different directions largely follow the coasts of the British Isles southwards, and to some extent westwards. In winter there may be further migration—local migration and immigration from the north and east—in the form of " weather movements " on the part of hardy species, but the occurrence and extent of these depends on the meteorological characteristics of the particular year.

Emigration from the British Isles is in a general southward direction, and takes place from our south coasts. It is mainly to France, Spain and Portugal, and beyond to Africa. A little of it has a more south-easterly trend, as the recovery of a few of our marked birds in Italy has shown.

In spring there is a great series of movements which are the counterparts of those just described for autumn. There is the departure of our winter visitors, the transit of passage migrants, and the return of the summer visitors. There is also local migration in the opposite direction to that of autumn. These spring movements are on the whole less evident than their counterparts. It is of course in autumn

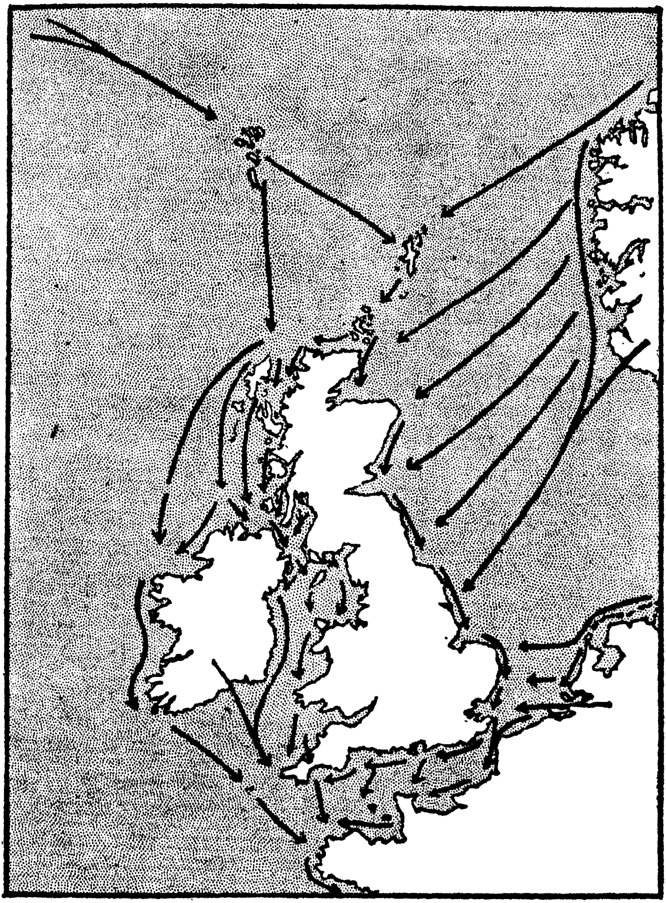


FIG. 8.—PRINCIPAL DIRECTIONS OF MIGRATION TO AND FROM THE BRITISH ISLES IN AUTUMN

Mainly after Eagle Clarke

The arrows are intended only to show the general directions of the chief movements in the area, and it is not to be understood that migration is confined to a few narrow routes. The directions followed in spring are similar, but of course reversed.

that the bird population is at its maximum, before the young of the year have been subjected to the heavy mortality which occurs in their first winter. There is also a greater tendency in autumn to linger before departure and during passage.

Migration Routes

We have so far been speaking of main trends of migration, and the general directions in which movements take place. It remains to deal with the question as to whether migrating birds follow definite routes, and, if so, of what nature. This has been the subject of a good deal of misconception in the past, and is still to some extent undecided owing to the difficulty of obtaining satisfactory evidence.

We can say with certainty that a great deal of migration follows the line of geographical features such as coasts and rivers, and that a preference is often shown for making sea-crossings at the narrowest points. It must not be hastily assumed, however, that the importance of such features lies in the aid that they can give in guiding migrants on their way: we shall revert to this aspect of the matter in considering the problem of orientation in a later chapter. Coastlines and river valleys have a value of another kind, in that for many birds they provide the best opportunities for obtaining rest and food during halts between stages of the journey. In the case of coasts this is particularly true of aquatic species, and of shore-birds which find on the sands and estuarine mud-flats their natural habitat. In the case of valleys the advantage must be greatest where the river passes through inhospitable country, consisting of high mountains or of desert: the Nile is an obvious instance. It may also be that we tend



[*R.A.F. Official Photograph, Crown Copyright Reserved*]

BIRD'S EYE VIEW OF A RIVER VALLEY

The Nile flowing between cultivated banks.

to over-estimate the part which such geographical features play as migration routes, merely because it is along their courses that it is easiest to make observations.

However that may be, it is also certain that much migration takes place on a broad front, over both sea and land, where there is either an absence of conspicuous geographical features running in the proper direction or a lack of apparent preference, on the part of the birds, for any particular features of that kind. We have already seen that a great autumn movement crosses the North Sea in a general south-westerly direction, to strike the eastern sea-board of Great Britain over a length of at least five hundred miles: similarly, the southward stream of migrants across the Gulf of Mexico is perhaps eight hundred miles in width. Again, the greater part of the continent of Europe is traversed by migrants in directions which have often no apparent relation to those of the main geographical features.

We must thus accept as facts the occurrence of migration following coastlines, river valleys and other features, and equally the occurrence of migration crossing sea and land on a wide frontage. It is sometimes suggested that these are really distinct kinds of migration, performed in different ways, but against this is the fact that the same species of bird may on occasion take part in both forms of movement at different times or places. The true conclusion seems to be, rather, that migration is not necessarily dependent on the existence of routes marked by coastlines and great rivers, but that there are valuable advantages to be gained by following salient features of that kind: the result is a great concentration of actual lines of flight where these

features are available and lead in suitable directions. Where these conditions are not fulfilled the concentration does not occur, and we find a more diffuse movement on a broad front.

Without at present going into the question of orientation, we may remark that overland migration on a broad front does not necessarily imply that the individual flight-lines are independent of landmarks of some kind, other than main geographical features such as have been mentioned. In flights of any length over open sea, landmarks are out of the question. Many such crossings are made, as we shall notice again more fully. There is nevertheless a tendency, as already mentioned, for migration to take place at the narrower points: thus, there is more migration across the Mediterranean Sea near its eastern and western ends and near the middle, than in the two intervening belts where the crossing is longer.

There is no scientific evidence to support the idea, which one often hears expressed, that the paths of migration across the sea follow the lines of sunken land-bridges belonging to former geological epochs. No doubt the two often coincide, as the sites of such former links are often where the existing land-masses are closest together, but the sea is traversed by migrants in many other directions as well.

CHAPTER V

THE SEASONS OF MIGRATION

Spring and autumn migration—A year's migration in the British Isles—Migration and climate—Migration and weather.

Spring and Autumn Migration

IT is usual to think of migration as something which takes place twice a year, and it conveniently expresses a general truth to speak of spring movements and autumn movements—the former towards the breeding area, the latter away from it. Nevertheless, migration is by no means confined to two short periods. We need not at the moment concern ourselves with the complication that migration within the tropics is related to seasonal changes of quite a different kind, or with the fact—affecting trans-equatorial travellers—that the ordinary seasons are reversed in the temperate zones of the Northern and Southern Hemispheres respectively. Even without going beyond Europe, we find that the seasons of migration are almost as extensive as they could possibly be.

For one thing, although migration is related to climatic change, the tolerance or requirements of different species vary greatly. Thus, there are species which reach their breeding grounds early and leave late—the two things usually go together—while others arrive late and leave early, spending only a small fraction of the year in their native area. In the British Isles, for instance, it is a familiar fact that the wheatear appears in March, the nightingale in April, and the swift mainly not until May.

Further, for any one species the dates when climatic conditions are suitable must necessarily differ widely between one part of its range and another, if its distribution be extensive. The swallow is a summer visitor to almost the whole of Europe: it reaches Gibraltar by the middle of February, southern France by the middle of March, England by the beginning of April, Scotland in the latter half of that month, southern Scandinavia during the first half of May, and the extreme north of Norway not until the beginning of June—these are average dates for the first large influx of migrants, neglecting the erratic appearance of early individuals. The relation between the northward spread of spring conditions and the advance of migration is not a simple one, however, and we shall return to it again. In autumn there are likewise differences between the dates of departure of any species from various parts of its summer range.

Even for a single species in one and the same area, arrival or departure is not completed in a moment, but is usually spread over several weeks. Each spring, for a particular species in a given area, odd birds are first reported from here and there; then a few are to be found almost everywhere; then numbers; and eventually the full quota is present. In this way there may be weeks between different individuals of the same species native to the same district: add to that the time taken on the journey, at which we can for the most part only guess, and it will be evident that even one section of the migration of a species may be of considerable duration.

Then again, the spring migration is scarcely completed before there occur certain summer movements which precede the true autumn migration. These are not usually of great length, but sometimes

involve journeys of a few hundred miles. They are performed particularly by young birds a few weeks old, belonging to species which breed early in the year. Lapwings, for instance, are sometimes on the move before the end of May and commonly in June: young starlings often travel quite long distances in June and July. The nature of these summer movements is not very clear, and is probably not the same in all cases. Sometimes they may represent an autumn migration performed very early, and sometimes merely the first stage of an autumn journey that will be continued later in the season. In other instances the movement seems to be a dispersal which precedes the true migration, and sometimes this displays a curious tendency in the opposite direction—a point to which further reference will be made.

After the completion of the autumn migration proper, moreover, there are the weather movements of which mention has already been made. These may occur at any time during the winter, according to the incidence of severe weather. Sometimes they happen when spring is well advanced and much return movement has already taken place. In this latter case they have the character of "reverse migrations", but it is not easy to be sure whether the individuals participating are or are not birds that have performed a normal spring movement.

~~We see, therefore, that~~ spring migration and autumn migration are both spread over several months; and ~~that~~ there are also summer movements and winter movements which largely occupy the intervals between. The seasons of migration are thus nearly continuous, so that there is scarcely any time of year when the bird population is wholly

stationary. Migration is nevertheless especially characteristic of a few months in spring and in autumn, when the principal movements are at their height.

A Year's Migration in the British Isles

We have so far been considering the seasons of migration from a general point of view, although with Europe more especially in mind. Let us for a moment examine the subject more closely with reference to a particular area, the British Isles. This country is indeed very favourably placed to serve as an example, because it lies midway between the arctic and subtropical extremes of Europe and sees something of the various principal aspects of migration. It is within the summer area of many species which are incapable of withstanding even a temperate winter; it is within the winter area of many hardy migrants which never penetrate far south; and it is within the passage zone of others which are merely transient visitors in spring and in autumn. It has, in addition, a great many species which are represented throughout the year, but of which individuals are migratory in greater or less degree. Let us, then, review the movements which take place within a period of twelve months.

The spring migration begins in February with movements within the British Isles of local migrants returning to their breeding grounds: these include movements from Ireland to Great Britain. If conditions are favourable the second half of the month will see some immigration from the south; and emigration—to the north, but more especially to the east—may also begin before the end of the month. In March the passage movements of species represented throughout the year are at their height,

and the first arrivals of purely summer visitant species are noted. There is also much emigration of winter visitors.

In April nearly all the remaining summer visitors begin to arrive, and there is also passage of these species—as well as continued emigration of winter visitors—to countries further north. In May the movements of summer visitors and birds of passage are at their height. In early June there is, in particular, still much passage of birds bound for the far north.

By the end of June the tide has already turned: in fact, some slight return movements are noted even earlier. In July migration gradually assumes considerable proportions. There are local movements, particularly of young birds, although in some cases these may be no more than a preliminary dispersal from the breeding grounds. Some summer visitors begin to depart, including adult cuckoos and the vanguard of the swifts. By the end of the month there is passage of young shore-birds from further north.

In August these movements continue, although still on a minor scale: the exodus of a few early species is practically completed. Emigration of summer visitors is at its height in September, and many species are not seen any later. Passage and immigration from the north increases, and similar movements from the east begin.

The autumn influx of winter visitors and birds of passage reaches its maximum in October, and the emigration of native birds is completed. These movements diminish during November, and before the end of that month true migration is practically at an end.

In December and January, however, there are

often " weather movements ", varying in time and nature with the meteorological characteristics of the particular year. These are mainly local movements, but immigration and emigration may also occur.

Weather movements sometimes occur still later, in February or March, thus overlapping the first manifestations of spring migration. In this way we may get " reverse migration ", which is probably merely local as a rule, although sometimes recorded on a greater scale. It is not known that any of the true long-distance migrants take part: the effect of unseasonable severe weather on these is usually purely disastrous.

Migration and Climate

The duration of the seasons of migration at a particular locality is naturally governed by climatic conditions. Thus, in the far north the seasons are very short. The Arctic spring is late, the summer brief, and the autumn early: the region is habitable for scarcely more than the few weeks which are necessary for mating, nesting, and rearing young. The birds arrive, reproduce, and depart: the position is thus a simple one, uncomplicated by the passage of birds native to regions beyond, or by the replacement of the summer visitors by hardier migrants from elsewhere. Migration has here reached its limit.

On the other hand, in the extreme south of Europe the spring migration begins very early in the year, as might be expected, but it also lasts very long. The native summer birds are soon established, and they have a long season before them. Through their area, however, there continue to pass for months longer the migrants that are bound for countries further north, where spring is tardier in its appear-

ance. This applies to some extent even to individuals of the same species: those which settle in the southern parts of the summer range may already be nesting while others are on their way through. Midway between the two extremes, in areas such as the British Isles, the position resembles that found further south; but the difference in date between the arrival of summer visitors and that of birds passing through is smaller, and the periods of these two movements commonly overlap to a large extent.

Enough has been said to make one principle clear. A species does not, as a rule, spread slowly like a great wave, keeping pace with the advance of spring and leaving some individuals to breed in every region over which it passes, until the last remnant is cast up at the extremity of the range. We know quite positively—and it is obviously a fundamental question—that migration does not happen like that. Rather is it a case of a succession of waves, each of which goes a little further than the one before and then subsides. The detachments of a species which are native to different regions thus play "leap-frog" over each other as they return to their summer localities. Those that have furthest to go must therefore start later, unless they come from further away. The second alternative may apply in some cases, but the idea that those which go furthest north also go furthest south is not tenable as a general rule: marking results show that individuals native to widely different areas may winter together.

A question which deserves further consideration is the rate of advance in the northward migration of any species, and the relation of this to the climatic conditions encountered. From what has been said it will be plain that this is quite a different matter

from the speed with which an individual bird accomplishes its journey, and still more so from the velocity of its actual flight. The rate of spread, as we may call it, is gauged by the average dates of the appearance of the species at different places.

Knowing that migration is adapted to climate, we might expect this rate of spread to keep pace with the advance of spring as measured by some such factor as mean temperature. The actual position is not so simple as that, and indeed differs as between one species and another. In some cases the migration seems to be closely adjusted to the seasonal differences between localities, while in others the spread is slower than the advance of spring. More commonly the birds outpace the season, so that as we go north we find the same species arriving at lower and lower temperatures. The rate of spread is commonly not uniform, moreover, but is in many cases accelerated towards the limit of the range.

Some dates for the influx of the swallow over Europe have already been given. Mr. Southern[1] has collected the available material and plotted isochronal lines at fortnightly intervals in comparison with the advance of spring as shown by the 48° F. isotherms for corresponding dates. There is a lag after the first arrival of swallows at Gibraltar in mid-February, and the movement starts in southern France, and on the south coast of Europe generally, in March. It is then behind the isotherm; but it catches up by the beginning of April, when the two show a remarkable conformity. By the beginning of June the movement is a clear month ahead. The spread of about 2,000 miles over the main part of Europe occupies 79 days: it is made at a fairly steady rate, averaging 25 miles a day, with a slight

[1] H. N. Southern (1938). In *British Birds*, Vol. 32, p. 4.

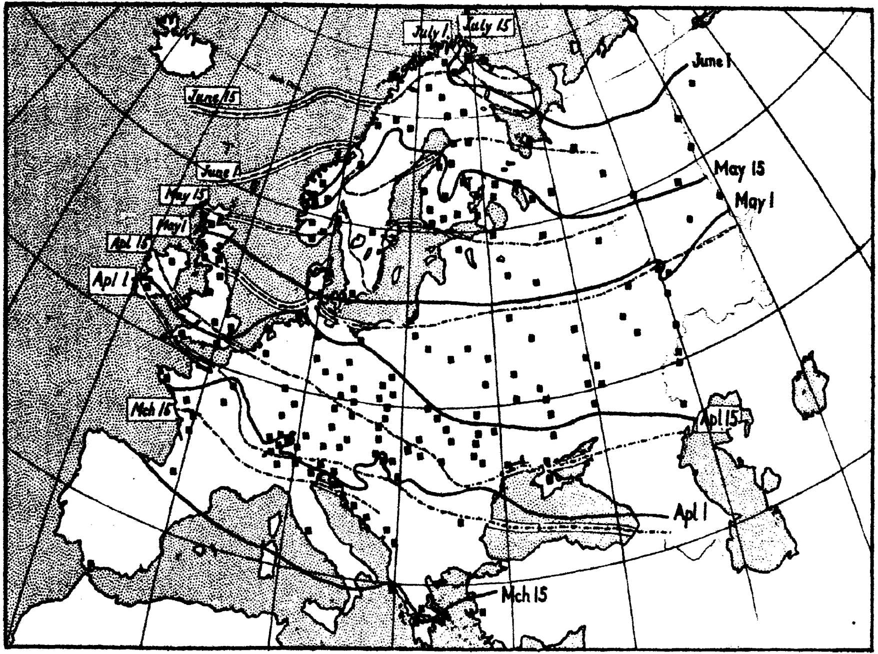


FIG. 9.—SPREAD OF THE SWALLOW OVER EUROPE IN SPRING

After H. N. Southern

The fortnightly isochronal lines, shown as continuous black lines and dated on the right-hand side, are based on average dates for the first large influx of swallows; each locality providing such a datum is shown as a black square. The interrupted lines, dated on the left-hand side, mark the progression of the 48° F. isotherm at corresponding intervals.

tendency to quicken in the western coastal region and to lag on the higher ground. The willow-warbler, similarly studied by the same author[1], shows a still more even rate of spread and closer conformity with the isotherms. The spread is mostly in advance of the swallow's (apart from the early arrival of that species at Gibraltar), but in the extreme north the two movements become almost simultaneous. On the other hand, the spread of the red-backed shrike[2] over Europe—mainly in a north-westerly direction from the eastern Mediterranean—is comparatively rapid and shows no correlation with the isotherms. Specially valuable evidence on this point has been obtained in North America, where it is probably easier than in Europe to collect date records on a uniform basis for the whole continent. The Canada goose is cited as an example of a migrant which spreads northward with the season, its advance being slow and regular and keeping pace approximately with the isotherm of 35° F. Thus it reaches Missouri by the middle of February, but Hudson Bay not until the end of April. The American robin spreads still more slowly. It takes seventy-eight days for the 3,000 miles from Iowa to Alaska, whereas the advance of spring crosses the same area in sixty-eight days.

An example of rapid spread is provided by the yellow warbler, which winters in the tropics. As Mr. Lincoln[3] says: "the birds reach New Orleans about April 5th, when the average temperature is 65° F. Travelling north much faster than does the season, they reach their breeding grounds in Manitoba the latter part of May, when the temperature is only 47°. Encountering progressively colder weather over their

[1] H. N. Southern (1938). *Tom. cit.*, p. 202.
[2] H. N. Southern (1941). In *British Birds*, Vol. 35, p. 114.
[3] F. C. Lincoln (1935). *The Migration of North American Birds*, Washington.

entire route, they cross a strip of country in fifteen days from May 11th to 25th that spring takes thirty-five days to cross. This 'catching up' with spring is habitual in species that winter south of the United States and in most of the northern species that winter in the Gulf States."

The same authority states that the spread of the blackpoll warbler is at the rate of thirty to thirty-five miles a day from the Gulf of Mexico to Minnesota. "Then comes a spurt, for a week later blackpolls have reached the central part of the Mackenzie Valley, and by the following week they are observed in north-western Alaska." During the latter part of the journey the rate is increased to an average of over 200 miles a day. In this way, thirty days are required for the advance from Florida to southern Minnesota, a distance of 1,000 miles, and scarcely half that time for the remaining 2,500 miles to Alaska.

It may be added that although the rate of spread of summer visitors does not usually keep level with the advance of spring, but more commonly outstrips it, a close relation is apparent. Thus, latitude for latitude, the arrival of the birds is earlier where the spring comes sooner, and the rate of spread is quicker where the advance of the season is more rapid. The adaptation to climate remains, even although there is not an exact adjustment to some particular temperature in each case.

Much less is definitely known about what we may call the rate of withdrawal in autumn, which is not necessarily the strict counterpart of the spread in spring. Autumn migration as a whole gives the impression of being more gradual and less urgent than spring migration, and the circumstances are not entirely analogous. In spring the urge seems to

be to reach the summer area and begin breeding at the earliest date possible for each locality. The birds which breed furthest south can thus complete their reproduction earlier in the season than those which breed furthest north, and this may affect their date of departure for winter quarters. It is therefore possible that the "leap-frog" principle does not apply in autumn to cases in which it certainly applies in spring: in that event the withdrawal will be a more gradual process, in which the birds already furthest south will go first and those further north will slowly follow. The truth is difficult to ascertain with regard to widely distributed species, although marking of individuals should eventually throw light on the point. It is known, however, that some of the species which breed only in high latitudes are among the earliest of autumn migrants: they not only leave their breeding grounds of necessity at an early date, but also reach places far to the south within quite a short time.

Migration and Weather

We have been discussing the relation between migration and climate, and have seen that it is a close one. The existence of some relation was of course obvious, as migration is undoubtedly a seasonal phenomenon. We may next ask what relation there is between migration and weather. At first glance the distinction may perhaps seem too subtle: actually, it is both simple and important.

Climate is average weather. The idea of climate is a generalization, built upon mean values for the weather conditions of a great many years. Weather is something that actually happens, and that is notoriously variable from year to year. Is it only to the average conditions, namely to climate, that

migration is adapted; or is its performance also adjusted to suit the weather of the particular year?

The answer to this question is not easy to give, and the information available is far from complete. It is certain that migration is affected by weather conditions to some extent, and varies from year to year accordingly. The effect, on the other hand, seems to be only a partial one, at least in the case of typical migration. The date of a movement is not determined by the weather, but is only retarded or advanced within narrow limits. Migration indeed appears to be more regular than the weather.

It has been clearly shown that it is the weather at the starting point of a flight that is important. This is what we should naturally expect, unless we romantically credit birds with mysterious foreknowledge of the conditions which they will meet at some distant place. In actual fact, we not infrequently find that birds arrive at most inopportune times, sometimes reaching their summer quarters when these are in the grip of some exceptionally late manifestation of winter. In other cases summer visitors may be overtaken by the unusually early occurrence of severe conditions before they have set forth on their autumn migration. Or, again, storms or delaying winds may be encountered during a flight which began under favourable auspices.

The result of such happenings is apt to be disaster. Long-distance migrants which arrive too soon, under the conditions of the particular spring, seem to have no tendency to retrace their flight. Delicate birds surprised by an early cold spell in autumn may become incapable of departure, as happened to vast numbers of swallows and martins in Austria and neighbouring countries in September 1931. Migrants encountering storms midway are

likely, if they are crossing the sea, to be overwhelmed. Sandstorms in the desert may be equally fatal.

Although the closest relation between the dates of migration and the weather is to be found at the starting point of a flight, it often happens that the same kind of weather prevails over a wide area. This accounts for an apparent connection, on occasion, between migration and the weather at the place of arrival. In a late season our summer visitors would not unnaturally be behind their normal times if relatively backward conditions extended to southern Europe. There is also a purely artificial effect on observation, in that new arrivals tend to escape notice under unfavourable conditions, when they are cowering in shelter rather than singing on high perches.

In a later chapter we shall return to the subject of weather, to discuss just what factors influence the date of a movement. For the present we are concerned only with the broad facts as to the seasons when migration takes place. Our general conclusion is that these seasons are closely adapted to climatic conditions, although in most cases not exactly to any one factor such as a critical temperature; and that they are subject only to slight modification in response to weather variations from year to year.

CHAPTER VI

THE METHOD OF MIGRATION

Nocturnal and diurnal migration—Altitude of flight—Speed of flight—Speed of migration—Duration of flight—Association and segregation.

WE have discussed the geographical aspects of migration, and its seasonal aspects: let us now consider the actual method of performing the migratory flight. Why do some birds travel by night and others by day? At what altitude do migrants fly, at what speed, and for how long at a stretch? These are among the questions that suggest themselves from this point of view.

Nocturnal and Diurnal Migration

As we have already noticed, a great deal of migration takes place by night. It is for this reason that so much of it passes unobserved, and that between one day and the next birds may appear abundantly in a locality, or disappear from it, without their actual flight being detected. This flying by night is very remarkable, as in the majority of cases the birds concerned are wholly diurnal in habit during the ordinary course of their lives, and in fact usually seem to be quite helpless in the dark. Yet nocturnal migration is the rule rather than the exception among the small songbirds, for instance. It is less surprising in the case of such birds as plovers and sandpipers, which are to some extent nocturnal at all times.

One of the purposes served by nocturnal migration is doubtless safety from attack by birds of prey, although one would think that other dangers would

at the same time be increased. Many of the species that always migrate by night are certainly small and weak birds, which usually depend on cover and are unaccustomed to making sustained flights in the open. On the other hand, larger birds such as crows, and strong fliers such as swallows, commonly travel by day, and we may perhaps assume that this is because they are able to do so in comparative safety. There are nevertheless exceptions enough to these general rules to show that this is not the whole explanation, and there are various species which sometimes migrate by night and sometimes by day. These last, however, include some of the diving ducks, which are said to travel by night when flying overland but by day when able to keep over the sea.

Another factor is that of opportunity for feeding. Long flights involve a great expenditure of energy, making it particularly necessary for the bird to feed well both beforehand and afterwards. For birds that need the daytime in which to obtain food, a nocturnal journey has therefore great advantage. Some diurnal migrants are able to feed during the journey: swallows, for instance, often travel in a leisurely fashion, circling round in the pursuit of aerial insects as they go. Hawks, too, may often be seen stopping to make a meal, perhaps at the expense of some smaller fellow traveller. In other cases birds that fly by day—geese for example—are able to feed at night.

Mention has been made of the attraction that lighthouses have for nocturnal migrants, which are often drawn to the beam like moths to a candle. This happens when the weather is misty, and the reflection of the rays from myriad drops of moisture gives a dazzling effect. Sometimes the birds dash themselves headlong against the glass; at other times

they merely flutter round until they become exhausted, when they are in equal danger of destruction if there is only water below. At some lights, rests have been constructed to give foothold until morning to birds which might otherwise fall into the waves. We have already noted that coloured lights do not seem to be dangerous. Bright illuminations on high buildings in cities have also been known to cause many casualties among birds migrating inland at night.

The Altitude of Flight

It was at one time thought that migrants commonly travelled at very great heights—20,000 feet or more—above the sea or land which they happened to be crossing. The grounds for this view were mainly theoretical and are now known to be largely false. It was supposed, for instance, that there was some physical advantage in flying in rarefied air: that the contrary is true is well known in these present days of aviation. It was also thought that the wider range of vision obtainable from a height was necessary for purposes of orientation, especially during sea crossings. A measure of safety from enemies was another imagined advantage; and human failure to detect migratory movements was conveniently explained away.

These propositions need not be discussed, as the question is one of fact and not of theory and we have nowadays a good deal of evidence upon which to decide it. In particular, observations made from aircraft during recent years have been collected by various authors. These show that it is quite exceptional to encounter any birds, migrating or otherwise, at great heights. There is now also a great body of observational data showing how much

migration takes place within the range of human vision from the ground. For birds the size of a rook that is not much more than 3,000 feet, and for smaller birds it is still less: in ordinary parlance, therefore, birds recorded as passing over "at a great height" are probably often no more than one or two thousand feet above ground level.

The general conclusion from all the evidence is that the great bulk of migration, whether by day or by night, probably takes place within 3,000 feet of the surface of the land or sea; much of it is certainly well below that height—a few hundred feet up, or perhaps just above the ground or water. Many species always keep low, and all birds tend to do so in stormy weather. When crossing the sea, small land birds may often be seen making their passage only a few feet above the crests of the waves.

Where the land is high, the absolute altitude of flight above sea-level is often much greater. Some migration crosses high mountain ranges, where even the lowest passes are at a great altitude. In the Alps, the Col des Hirondelles—the crest of which is 11,370 feet above sea-level—takes its name from the finding of a dead swallow on the snow. That birds can live at very great heights is known from many observations not concerned with migrants: it was recorded on one of the Mount Everest expeditions that Alpine choughs followed the climbers to all the high camps, even that at 27,000 feet.

It is noteworthy that even when migrants are compelled by mountains to fly at a considerable altitude, they often descend to lower levels as soon as the configuration of the land permits. This tendency is well illustrated in a description by Major Cheesman[1] of an incident in the migration of the

[1] R. E. Cheesman and W. L. Sclater (1935). In *Ibis*, XIII Series, Vol. 5, p. 151.

swallow observed by him in north-western Abyssinia. "On the top of the northern precipices of the Simen Mountains I saw one of the comparatively few outstanding cases of migrating flocks that has come into my experience. This was at an altitude of 10,000 feet; below me the cliffs fell sheer, 2,000 feet at least; in the distance, to the north, lay the Takkaze River valley (3,300 feet), and beyond that the higher country of Eritrea. As I watched, flock after flock of swallows were hurrying northward; it was May. The migrating flight of the swallow differs from his fly-hunting cruise in settled quarters, where he gracefully glides and swoops on motionless wings. On Simen each bird was flying straight as an arrow, with continual wing-flapping, presenting a very businesslike appearance. Each flock on reaching the edge of the precipice launched itself over and dived down; in a few seconds they were out of sight, thousands of feet below. They had a 10,000 foot elevation, which they could have maintained over the low country beyond had they wished, but they lost it."

Speed of Flight

Extravagant notions were also at one time held with regard to the velocity of migration flight. It was thought that something quite out of the common was achieved, but the belief was based on speculative assumptions which we now know to be erroneous. In actual fact, the pace of migration is that of the unhurried flight of ordinary life. The accelerated flight of which birds are capable when pursued or pursuing can probably be maintained only over a short distance, and anything still faster is doubtless quite impossible. Most observers are indeed agreed as to the deliberate nature of migration flight, and

where actual measurements have been made with suitable instruments the tale is the same.

What are some of the actual speeds recorded by exact measurements? Colonel Meinertzhagen[1] puts the average ordinary velocities, used on migration, as follows:—smaller song-birds, 20-37 miles per hour; crows, 21-45; starling, 38-49; falcons, 40-48; most of the plover family, 40-51; geese, 42-55; and ducks, 44-59. The same authority quotes observations made from aeroplanes, by pilots who had watched their speed-indicators while keeping level with the birds (in the days of machines much slower than those to which we are now accustomed). White storks were thus encountered migrating at 48 miles per hour, at 4,200 feet, and wild-duck at 50 miles per hour. Swifts, not on migration but feeding at 6,000 feet, easily passed and circled round an aeroplane doing 68 miles per hour.

We have, of course, been speaking of absolute velocities, or " air speeds ". These are the figures recorded from the ground on windless days, or from an aeroplane under any conditions—machine and bird being equally affected by the wind. The actual speed in relation to the ground must always depend on the force and direction of the wind to which the bird is subject. The bird forms part of the body of air in which it flies, and its movement is relative to the movement of that air: it cannot even feel the wind, but only the head-on resistance to its own passage. The case is similar to that of a swimmer in a tidal current, who cannot judge his true progress except by reference to fixed objects.

A bird with an air speed of 40 miles per hour flying with a 25 miles per hour wind behind it, will thus travel at 65 miles per hour in relation to the ground: but if it turns round it will accomplish no

[1] R. Meinertzhagen (1921). In *Ibis*, XI Series, Vol. 3, p. 228.

more than 15 miles per hour. A side wind will also retard its actual progress: that is true whether the bird flies in a curve heading continuously towards its goal, or whether it makes good its lateral drift as it proceeds by turning partially towards the wind. The case resembles that of a boat ferrying across a running stream. Winds are of course seldom uniform, and in gusty air the bird will momentarily feel some effect as it passes from one current to another differing in speed or direction—and the same is true of the instant in which it makes or loses contact with the ground.

Although the direction and force of the wind so greatly affect the ease and speed with which a given distance can be covered, it is not found in actual fact that the performance of migration is very dependent on these. The same movements take place, on different occasion, with the wind in every quarter. Strong winds, irrespective of direction, are characteristic of weather which is generally unfavourable to migration. The suggestion that advantage is not taken of strong tail winds because these uncomfortably disturb the bird's plumage is based on a misconception of the physical possibilities: the bird's speed is added to the speed of the wind which bears it, and, as we have just seen, the effect which the bird feels is always that of a head wind.

A good deal of attention has been drawn of late to the frequency with which certain movements are performed against the wind. There may be reasons in these cases why the conditions which produce contrary winds are favourable to migration, but to some extent the explanation may lie in the conditions of observation. In windy weather migrants tend to fly low, and when flying against the wind they take longer to cross the field of vision: the movement is

thus more noticeable. Further, a sea-crossing which would otherwise be completed by night may be lengthened so that a landfall is made in the daytime.

Speed of Migration

We have so far been speaking only of the speed of flight, as distinct from the speed of migration. The velocity of the bird's actual passage through the air is one thing; the rate of its progress on a long journey, which may include many stops, is another. As regard this rate of progress it is difficult to obtain much reliable information, because so many different factors are involved. For the purposes of an estimate we should need to know the speed of flight, the effect of the prevailing winds upon it, the duration of flight at each stage, and the length of the stops between them: two of these points have already been discussed, and the other two will be considered presently.

Little help is to be derived from the rate of spread of a species, when it begins to repopulate in spring a region from which it has been absent during the winter. That merely gives us a minimum figure, which must obviously be at least equalled by the progress of individual birds. The probability, in most cases, is that it is greatly exceeded. As we saw in the previous chapter, the birds which go furthest north commonly start later: although a species may be three weeks later in its appearance in the north of Scotland as compared with the south of England, the distance may well be covered by the individual birds in as many days.

Only occasionally is a ringing result likely to throw much light on the question. It is too much to hope that a bird will often migrate immediately it is marked and chance to be reported immediately on

arrival at its destination! Nevertheless, there are a few interesting records, such as that of a mallard ringed in Wisconsin in November and recovered five days later in South Carolina, a distance of 900 miles in a direct line. This, of course, gives us merely limits of time within which the journey must have been performed, and the actual rate of travel may well have been greater than an average of something under 200 miles a day. Another record is that of a turnstone caught at the Heligoland lighthouse during a September night and released at 11 a.m. next day. Twenty-five hours later it was shot at Quineville, on the north coast of France not far from Cherbourg, about 510 miles distant in a direct line: there was little wind at the time. Whether this journey was done in a single flight or in at least two, and how much of the time represents stops, it is obviously impossible to say.

Of the length of the stops made betweeen different stages of a long journey there is little precise knowledge. Mr. Middleton[1], ringing birds of passage in Pennsylvania, has found that the average length of stay (as shown by re-appearance in his traps) varies from 2.33 to 7.45 days for different species. Sometimes the pause is merely for a day between two nocturnal flights, as is often evident to the observer who is able to keep the changing population of a small island under constant review. At other times the movement may be held up for several days by adverse conditions. In more favourable circumstances than such a place usually presents, however, it may be that pauses of some length are commonly made even when there is nothing in the external conditions to prevent an earlier resumption of the journey. We get the general impression,

[1] R. J. Middleton (1939). In *Bird Banding*, Vol. 10, p. 145.

nevertheless, that true migration is performed under a strong urge and that there is little lingering on the way; a more leisurely progress is doubtless characteristic of dispersals and wanderings.

Duration of Flight

It is a little easier to deduce something about the duration of single flights forming part of migration journeys. The total lengths of some journeys run to several thousand miles, but it is probable that the separate stages are fairly short as a rule. Most observers are agreed that migration is not usually maintained for the whole of a day or night: in the case of diurnal movements, it is at many different places commonly confined to the earlier part of the day. Assuming a flight of from six to eight hours, and a speed of from 30 to 40 miles per hour, we arrive at figures ranging from 180 to 320 miles; these are probably quite usual, and still shorter distances are likely to be covered against strong winds.

Many stretches of uninterrupted sea which migrants are known to cross do not necessarily involve much longer flights than these. The North Sea and Mediterranean crossings probably do not exceed 400-450 miles, and many are much shorter. The Gulf of Mexico, however, is crossed in directions involving flights of 500 miles and over, even by so small a species as the ruby-throated humming bird; and the New Zealand birds which cross the sea must necessarily make flights of 600-900 miles.

Greater distances than these can be achieved in a single flight on occasion, and are indeed regularly covered by some birds. The eastern form of the American golden plover breeds in northern Canada and the Arctic lands beyond. In autumn the birds come south-eastwards through Labrador, and then

from Nova Scotia they strike south across the Atlantic Ocean to South America. This must often involve a non-stop flight of some 2,000 miles, although some birds alight at Bermuda, the Bahamas, or the Lesser Antilles, on occasion. Still more remarkable is the case of the Pacific form, which breeds in western Alaska and north-eastern Siberia, and is a regular winter visitor on the uplands of the Hawaiian Islands. To reach these from the north, by whatever route, must involve a journey of *at least* 2,000 miles across open sea. The winter quarters also extend to Australia and New Zealand, but part of the migration takes place down the eastern seaboard of Asia.

There is also, as an example of an exceptional occurrence, the remarkable transoceanic flight by a large flock of lapwings, in December 1927, from Europe to Newfoundland, about which Mr. Witherby[1] has collected all available information. The species is ordinarily unknown in America; and the birds presumably came from Great Britain, as they included one which had been ringed in Cumberland as a chick in the preceding year. This would involve a flight of some 2,200 miles, which could have been accomplished in about twenty-four hours by aid of the strong easterly wind then prevailing (estimated by the Meteorological Office at an average of fifty-five miles per hour, at a height of 1,000 feet, almost directly behind the birds practically the whole way across). It seems probable that the birds were aiming for Ireland, to which there is a regular migration of this species, and overshot the mark by reason of this strong tail-wind. Even supposing that the birds actually set out from the west coast of Ireland, the shortest possible crossing would have

[1] H. F. Witherby (1928). In *British Birds*, Vol. 22, p. 6.

necessitated a flight of not much less than 2,000 miles.

Association and Segregation

The general tendency is for birds to be gregarious on migration, often much more so than is usual for the particular species at other times, and the numbers travelling together may be immense. There seems to be no general rule, but some species are especially apt to form vast flocks, while others—equally abundant—are more commonly split up into smaller parties. Some birds are generally solitary travellers, such as various birds of prey, but even these may band together when they are numerous. Flocks of migrants sometimes consist entirely of birds of a single species; sometimes mixed assemblages are formed, of birds of similar size, habits, and powers of flight.

The composition of flocks as regards the age and sex of the individual is subject to many differences. Among geese, for example, the flocks in which the autumn migration is performed seem often to be simply aggregations of complete family parties, thus including adults of both sexes and young of the year. Among ducks, on the other hand, it is common for the adult males—which have a moult in summer and perform few parental duties—to form flocks by themselves, while the young of both sexes accompany the females.

Among the song-birds, it is common for the parents to drive the young away as soon as the latter are able to fend for themselves. Migratory flocks consisting entirely of young birds are thus formed. Among the plovers, also, separate migration by young birds is not unusual. In the case of the cuckoo, the adults leave our shores in July, while

the young are mainly still in the care of their foster-parents of other species, themselves often non-migratory. The same is true of some other species of cuckoo, including the two which are native to New Zealand. That country is also the breeding place of the sooty shearwater, which "winters" in the North Pacific and North Atlantic Oceans while it is summer there. All the adults are said to have departed from New Zealand waters, on this long migration, a month before the young are ready to leave the nest and follow them. As in the case of some other petrels, these young "mutton-birds" are very fat and do not require to be fed at this stage.

In spring, the males of many species of song-birds reach the breeding area before the females, and establish themselves in their nesting territories to await the arrival of mates. Whether they leave the winter quarters sooner, or whether they travel more quickly, is not known: but migratory flocks consisting entirely of males may often be seen in cases where the sexes are readily distinguishable in the field. Among plovers and ducks it is usual for the sexes to reach the breeding grounds together, and the birds are often mated before they arrive.

Many migrants call incessantly during flight, and in the dark this doubtless helps to keep the flocks together. Some diurnal migrants are also vociferous; but, on the other hand, the silence of crows, for example, may be very noticeable as great flocks pass overhead by day. Many birds sing in their winter quarters, or at stopping places on migration—especially in spring: the nightingale does, for instance, both in West Africa and while passing through Egypt.

PART III
GENERAL FEATURES OF MIGRATION

CHAPTER VII

THE IMMENSITY OF MIGRATION

The prevalence of migration—The abundance of migrants—The extent of migration—The period of migration—The individual rôle.

HAVING first considered the broad facts of bird migration, and then examined in more detail some aspects of the phenomenon, we may now review the subject in order to formulate some general impressions. These should serve usefully as a basis for the concluding discussion of theoretical problems.

Our first impression, after an introduction to the facts of the case, must surely be of one immensity. The magnitude of migration is seldom realized by the casual observer. The phenomena are apt to be regarded as characteristic of a small minority of birds, to be specially classed as migrants; as affecting only certain parts of the world, wherein seasonal changes are strongly marked; and as restricted to short transitional periods, in spring and in autumn. Closer study reveals a very different picture, in which migration is seen to take place on a vast scale.

The Prevalence of Migration

Migration is indeed very far from being the peculiar characteristic of a few species, but is widespread among the great natural orders into which

birds are classified on the basis of what appear to be their evolutionary relationships.

We find, for instance, that migration is developed in the highest degree in some of the insectivorous song-birds. The swallow is the proverbial example of a migrant in popular thought, and it is in fact an excellent type of the truly migratory species which performs regular movements over great distances: we have had repeated occasion to cite it in these pages. Other cases which at once spring to mind are the warblers of various kinds which fill our countryside with song at the beginning of summer. Other insectivorous migrants, belonging to groups quite different from those just mentioned, are the swift and the cuckoo: both of these are real long-distance travellers.

Less familar to the general public, but in fact just as good examples, are birds of the plover and sandpiper group—the so-called "waders", or "shore-birds" as the Americans have it. Many of these are migratory in the very highest degree, performing journeys from their breeding-grounds in high northern latitudes to the extremities of the southern continents. The knot is an example of a sandpiper of which this is true, and the remarkable transoceanic flights of different kinds of golden plover have already been mentioned.

Another group of notable migrants is that of the terns, which thus have an additional claim to their popular title of "sea-swallows". Terns of several species are among the greatest of travellers and are all wholly absent from even the temperate latitudes of the Northern Hemisphere during the winter. In the case of the Sandwich tern, there are many records of birds ringed in Great Britain, and elsewhere in Europe, being recovered on the coasts

of West Africa and South Africa, and even round to Natal.

Many other kinds of birds are great migrants. We find examples among the geese and ducks, among the birds of prey, among the herons, among the pigeons, and so on. In the countries where it is known—which unfortunately do not include our own—there is no more striking case than the white stork, of which some mention has already been made in an earlier chapter. In parts of Europe this large bird is a nester on the house-tops, but its winter quarters extend to South Africa, and the actual passage of its flocks—in the Levant, for instance—is often conspicuous.

There are certainly groups which we rightly think of as composed characteristically of sedentary species. The game birds (in the ornithological, not the legal sense)—pheasants, partridges and grouse—are a case in point. Very many of the members of this order are non-migratory: these include species found in high latitudes, such as the Spitzbergen ptarmigan, which survives the Arctic winter in burrows beneath the deep snow. Nevertheless, this same group contains so notable a migrant as the quail.

As might be expected, it is among the orders which are represented for the most part only in the tropics that migration is least in evidence. Here again, however, it is easy to quote exceptions. Most of the numerous species of humming-birds are found in the tropical parts of the American continent. They are minute and apparently delicate birds, and their extraordinary darting and hovering flight—like that of insects in its speed of wing-beat and in its erratic course—suggests anything but the power of sustained effort in a definite direction. In spite of this, we

find that a few humming birds are in fact regular migrants, performing long journeys. There are, for example, the ruby-throated humming bird, which comes north each summer as far as eastern Canada, and the rufous humming-bird, which breeds in north-western Canada and winters in tropical Mexico.

At least among the flightless birds one might expect to find that migration did not occur. Yet, in a sort, it does. Various species of penguins that breed on the coasts of the Antarctic continent have to spend the winter hundreds of miles further north in order to find open water, free from pack-ice. As we have seen, they return in spring to their vast " rookeries ", swimming most of the way but often completing the last few miles on foot across the solid ice which still fringes the shore.

The number of species showing some degree of migratory movement is thus very great. It is by no means limited to those which perform journeys of spectacular extent, or which are wholly absent from their native area for part of the year. It includes all those which move in lesser degree, possibly only locally within their general area, from inland districts to the coasts or from mountain to valley; and those of which some individuals are migratory, while others of their species are permanently resident.

Abundance of Migrants

While the species which take part in migration are to be counted in thousands, the individuals of even a single one of them often amount to untold millions. The movement of one species at a particular place during a single day sometimes involves the passage of vast hordes of birds.

Thus Gätke[1] wrote: "October brings to the shores of Heligoland not only the largest variety of species, but also by far the largest numbers of individuals of any period of the year. Throughout the whole of the month, hooded crows travel in never-ending swarms of hundreds and thousands across the island, and for a breadth of many miles past both its coasts; cloud-like masses of starlings pass at the same time. At the beginning of the month, if the weather is favourable, the island literally teems with song-thrushes, especially during the morning hours. The number of skylarks passing during dark nights across and past the island in one endless stream defies even approximate computation."

Numbers are especially impressive when we have to do with birds of large size, such as storks, cranes, or geese. The blue goose has its breeding grounds north of Hudson Bay, and nearly all the members of the species apparently winter on the salt marshes of Louisiana, bordering the Gulf of Mexico. Here enormous numbers congregate, especially just before their northward departure about the end of March. Mr. McIlhenny[2] described the main concentration on one occasion as follows: "We found the flock to be solid for a distance of two and a half miles, and from one half to three-fourths of a mile in width. In riding through it, the geese were so tame that they would not take wing, simply walking away from the horses a few feet to the side of the path, and all the time we rode through the flock there were geese within ten or fifteen feet of us on both sides. We estimated this flock to contain from one and a quarter million to one and a half million geese."

[1] H. Gätke (Eng. trans. 1895). *Heligoland as an Ornithological Observatory*, Edinburgh.

[2] E. A. McIlhenny (1932). In *Auk*, Vol. 49, p. 279.

This observation was made on March 25th, and three days later practically the whole of this vast concourse set forth during a single afternoon and night.

Even in the British Isles, geese of various kinds are to be found in tens of thousands during the winter in a few suitable places, and their migration at times provides a wonderful spectacle. Mr. Berry[1] has described the flocks of pink-footed and other geese which visit the Firth of Tay, on the east coast of Scoland, on spring passage. Thus, on April 28th, "The first geese were spotted at 05.56 hours, from which time pack after pack were seen going north-north-east at a great height. . . . At 07.05 hours, while having a hurried breakfast, I heard the yelling of a very large number of geese, and jumping on deck saw line after line of them coming over the hills to the south. . . . It was now a perfectly glorious day, and V's of geese were visible at a stupendous height. The majority went straight on for the most part in complete silence, but every few minutes one bird would call, and then for a minute every gaggle joined in and the noise was impressive until, as suddenly as it had begun, it ceased." Then, after a break of twelve hours, another wave of migration began in the evening, many of the birds descending. "For the next hour and a half we could only gasp helplessly with amazement—the numbers of geese passed all hope of computation. I had no idea there were so many geese in the entire British Islands; even the thousands on Loch Leven at the beginning of October were negligible compared to these hordes, which extended literally for miles. There were geese paddling about on the shallow pools, geese sitting asleep on the sand-banks, and acres of geese feeding on the young shoots of reeds and rushes which flank the river in a broad belt for a dozen

[1] J. Berry (1931) In *Scottish Naturalist*, 1931, p. 141.

miles in that district. Poling our boat up a creek we put up eight bean-geese at twenty yards, which jumped a pack of at least 2,000 greylag half a mile further on. There followed a thunderous roar of wings as pack after pack of geese rose and swung round and round, all yelling their hardest."

An impression of the numbers that take part in migration may also be obtained from the magnitude of the disasters that sometimes occur. On one occasion, during an autumn snowstorm, large numbers of migrants crossing Lake Huron were forced into the waves. Afterwards, on one section of the beach the dead cast up were estimated at five thousand per mile. During a spell of late wintry weather one spring, it was estimated that three-quarters of a million Lapland buntings, or "longspurs", were lying dead on the ice of two lakes in Minnesota, each about a square mile in extent, and dead birds were reported in greater or smaller numbers over an area of more than 1,500 square miles.

In the catastrophe which overtook swallows and martins in central Europe during the cold spell in September 1931, hundreds of thousands of birds must have perished. Those which were successfully secured and restored under the auspices of the organization for bird-protection in Vienna, and transported by aeroplane for release at Venice, numbered about 89,000. These can have represented no more than a fraction of the total. A decrease in the breeding population was recorded in the following year in eastern parts of Germany.

The Extent of Migration

That migration is not confined to any particular regions, but is in fact of world-wide occurrence, we

have already seen. In the Arctic regions of Europe, Asia and North America we have a zone from which nearly all birds depart in winter. In the temperate parts of the same continents we find that many birds leave, while others stay, and still others come from further north. In summer, in addition to the return of the breeding birds, northern temperate latitudes are visited by a few oceanic species native to the Southern Hemisphere.

In the tropics of Africa, Asia, Australasia, and America, we find the winter quarters of many species from both north and south. The tropics are also areas of passage for many transequatorial migrants, and among the native birds movements take place of rather a different kind from those known in higher latitudes.

In the temperate zones of southern Africa, Australasia and South America, many birds are summer visitors which migrate in autumn to the tropics. Here also we find those transequatorial migrants which have just been mentioned, "wintering" in the southern summer. Finally, on the Antarctic continent we have again a region which is almost deserted in winter, even by the great majority of its penguins.

Not only does some aspect of migration affect every part of the world, but there are single species with movements of tremendous range, and individual birds that perform journeys of extreme length. Some birds which travel from northern Europe to South Africa cover from six to seven thousand miles in each direction. There is not only distributional evidence to show that these journeys must be regularly made, but many ringing records for such species as the swallow and the white stork which prove the fact for particular individuals.

Birds which fly from the Arctic to Patagonia or New Zealand travel from eight to nine thousand miles.

Even these performances are outdone by the Arctic tern, which breeds in the far north and during our winter visits Antarctic seas. This gives it a latitudinal range of some eleven thousand miles; and, as the breeding area does not extend very far south in the northern temperate zone, at least some of the individuals must traverse the greater part of the area. We have already noted that the Atlantic is regularly crossed by this species, and that a ringed bird from eastern North America has been recorded from South Africa. It has been pointed out that birds which fly from Arctic to Antarctic, spending the summer in each, must be unique among animals in the amount of daylight which they enjoy during the year.

It is not only as regards distance from north to south that the migration ranges of some species are remarkable. Among the waders native to the far north, for instance, there are several which spread very widely over the earth. The turnstone and the sanderling both have a circumpolar breeding distribution, confined to the highest latitudes. The former migrates regularly as far as the coasts of South Africa, New Zealand, and Chile; the latter to those of South Africa, southern Australia and Patagonia. It is indeed a remarkable result of migration that birds which are at the time of reproduction restricted to a narrow belt, fringing the north polar regions, should during the rest of the year be distributed to the shores of the six continents.

The Period of Migration

Consider, again, that migration is not restricted to two short seasons in spring and in autumn, but

that in fact its manifestations extend practically throughout the year. Seasonal changes differ from one region to another, so that the appropriate dates for arrival or departure vary widely with locality. We have seen, also, that some species are early migrants, and some late; and that there are summer movements and winter movements, of one kind or another, between the main seasons of typical migration. Even the movement of a single species in a given area may be of considerable duration, weeks often elapsing between the coming or going of the first individuals and the last. The period of mere arrival or departure, moreover, is apt to be extended by passage movements of other members of the species which are on their way through to other areas.

With all these factors together, migration as a whole is an almost ceaseless tide, with scarcely a pause at its turn twice a year. Even at these times of relative stability in the bird population of a given locality, it is necessary only to change the point of observation to some other part of the world in order to find active movement in progress.

From the point of view of the individual bird, too, the period of migration is often extensive. We cannot be very sure how long particular journeys usually take, but it is evident that some of the greater ones must occupy a few weeks even if no long stops are made: from first to last they doubtless often take much more, and that represents only half of the double journey. We may note, also, how small may be the interval between two long migrations, in the case of birds which breed during the brief summer of high northern latitudes: the native area is tenanted for little longer than is necessary for bringing a new generation into the world, and

within that time the young have to be ready for their first journey.

The Individual Rôle

Possibly, indeed, it is in this individual aspect that migration most truly shows its magnitude. Spectacular in numbers, ubiquitous in extent, ceaseless in duration, the phenomena are perhaps even more impressively immense in the rôle for which they cast the individual bird.

In migrating half across the world and back, a bird must occupy a considerable portion of the year in this process of changing its habitat. In covering annually some twelve or fifteen thousand miles, or more, it must expend a vast amount of energy. In facing all the perils of the journey, it must add greatly to the hazards of existence. The whole performance, too, implies the development of this function to a high pitch of perfection. The part which migration plays in the bird's life is tremendous, and the cost is heavy.

CHAPTER VIII

THE COMPLEXITY OF MIGRATION

Differences between species—Differences between communities—Differences between individuals—Differences dependent on age or sex—Geographical complexities—Seasonal complexities.

IF the phenomena of migration are vast, they are also exceedingly complex. So much may, indeed, be inferred from many things that have already been said in earlier chapters; but it will be useful to bring together here some of the points which illustrate this complexity.

Differences between Species

We have already seen that there are various types of migrants, presenting every gradation between the completely sedentary bird and the long-distance traveller. There are purely local migrants, moving only within narrow limits; and vertical migrants, which merely change the altitude at which they live on the mountain-sides. Then there are birds which disperse between one breeding season and the next, rather than move in any particular direction, and others which perform more or less erratic wanderings. Coming to the birds that show more definite migrations, we find that some remain within the influence of the temperate winter, and are often subject to further movements under stress of very severe weather later in the year. Others, on the contrary, avoid winter altogether by taking refuge in the tropics, or, in the extreme case, by crossing

the equator into the other hemisphere. Finally, there are birds which exhibit occasional irruptions at irregular intervals, and which we do not regard as migrants in the true sense.

It is not, of course, surprising to find migration developed in various degrees by species differing in their modes of life or in the climatic conditions to which they are subject. It is more difficult to understand why there should be great differences even among species which resemble each other in their general habits and live in the same parts of the world. Yet such differences are common, and are often found between closely related species. The birds may differ as regards being migratory or sedentary; as regards the direction and length of their journeys; and as regards the time and manner of performance.

In the British Isles about a dozen species of warblers are regular summer visitors: as a group they are characteristically migrants, and they certainly seem little fitted to endure our winter climate. Yet there is one, the Dartford warbler, which is a permanent resident, remaining throughout the year. Again, we have two closely related and in many ways similar species in the blackbird and the ring-ouzel. The former is present at all seasons, whereas the latter is purely a summer visitor. The contrast between the herring-gull and the lesser black-backed gull has already been drawn.

Even where two closely related species both fall in the same category, minor differences will almost always be readily found between their movements. Thus, the chiffchaff and the willow-warbler are both regular migrants, visiting the British Isles in summer, but the former is about a fortnight earlier in the date of its arrival here in spring. It would merely be

tedious, however, to multiply examples of differences between one migratory species and another—related or not—in respect of the directions, distances and dates of their movements.

Differences between Communities

The complexity goes much deeper than mere differences between the migratory behaviour of similar species. There are often differences in this respect among the members of a single species inhabiting various parts of the total range. The individuals in one area may be migratory while those in another remain stationary: or there may be differences in the migration performed.

Examples are particularly easy to find among British birds. In the temperate climate of the British Isles many species remain throughout the year, although they are mainly summer visitors to northern parts of the Continent. In such cases the British native individuals are often quite stationary, or at most perform local movements within the country; the continental birds, on the other hand, are migrants; many of which find winter quarters in the British Isles. The native starlings and mallard are resident, but their numbers are much increased in winter by immigrants from the north or east, while other individuals from these regions go further south on the Continent itself. In some cases the continental birds represent a separate sub-species or geographical race, distinguished by small differences in structure or plumage which are usually not apparent to the field observer. The tiny goldcrest is a migrant of which large numbers come to the British Isles across the North Sea in autumn: these birds belong to a continental race, different in some respects from the native one which is with us throughout the

year. Similarly, there are British and continental forms of the great tit, the latter coming to us as a migrant.

Between birds of a single species inhabiting different areas there must obviously often be wide variations in the movements performed, and more especially as regards their dates. A radical contrast in the directions followed is more surprising. A striking example of this is provided by the case of the white stork, about which a great deal is known as the result of ringing young birds on the nest. The birds native to eastern Germany migrate in autumn in a south-easterly direction through Europe, to Asia Minor and Syria: the route continues southwards through the eastern half of Africa. In western Germany, on the contrary, the direction of the autumn journey is south-westwards through southern France and Spain.

Individual Differences

In not a few instances the complexity goes still further, and we find that even in one and the same area the members of a single species may behave differently as regards migration. In Great Britain the song-thrush is a good case in point. Many of the native individuals remain through the winter—and, incidentally, are joined by visitors from the Continent—but others are quite definitely migrants, travelling to southern Europe.

The distances covered by the migratory individuals may vary. Thus, the lapwings native to Scotland and northern England are mostly summer visitors, although some remain through the winter. The results of ringing have shown that many of the migrants go to Portugal, but that many others go no further than Ireland.

It may even happen that entirely different directions are taken by individuals of the same species inhabiting a particular area. In the case of the white stork, just mentioned, there seems to be no clear demarcation between the breeding ranges of the south-easterly and south-westerly migrants respectively: apparently there is an intermediate area from which some leave in the one direction and some in the other. Similarly, of wigeon ringed as ducklings in Iceland, some have been found to make for Europe and others for North America. Birds of this species native to Russia, as far east as the Ural Mountains and the Caspian Sea, have been shown to migrate westwards, reaching the British Isles, while others from western Siberia fly south to India: whether there is any clear line of demarcation is not yet known.

One would like to know what part heredity plays in these differences between individuals, where species and area are the same, but the facts are difficult to ascertain. Are there, perhaps, races or strains within the species, differing in behaviour rather than in any more obvious way? If so, what is the effect of the inevitable interbreeding? Such evidence as we have is against this view, but it is admittedly scanty. The question can be approached only by comparing the movements of marked birds which are members of the same brood, or which are in the relation of parent and offspring. It is also important, but rather difficult, to ascertain whether a given individual tends to behave in the same way in successive years.

Some light has been thrown on this question as the result of an intensive study by Mrs. Nice[1] of a community of song-sparrows in Ohio, using coloured

[1] M. M. Nice (1937). In *Transactions of the Linnaean Society of New York*, Vol. 4, p. 1.

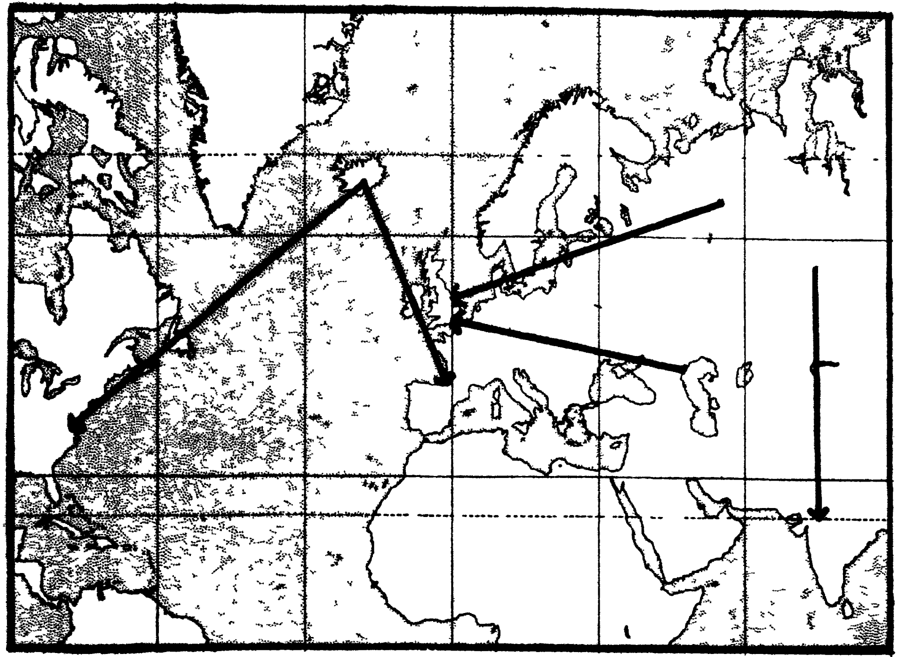


FIG. 10.—SOME DIRECTIONS OF WIGEON MIGRATION

A diagrammatic representation of some of the chief directions of autumn migration which have been shown by records of ringed wigeon.

celluloid rings as well as numbered metal ones and combining systematic trapping with close observation. This community consisted partly of residents and partly of summer visitors, and it was found that the majority of individuals retained the same migratory status from year to year, but that a minority showed change in this respect. As regards heredity, it was established "that seven resident fathers had seven resident sons, and that four migratory fathers had four migratory sons. But two resident fathers had two migratory sons and five migratory fathers had seven resident sons." Again, "four migratory pairs had migratory daughters; two resident males and migratory females had three migratory daughters, while two other pairs of the same combination had two resident daughters; a resident pair had a resident daughter." It was therefore concluded, in respect of the community under study, "that the difference between migrating and non-migrating is not a matter of inheritance." Also, "the fact that seven birds changed their status shows that the character is not a hard and fast one."

An irregularity which the present writer has termed "abmigration" has been revealed by the results of ringing. It probably occurs exceptionally among birds of many kinds, but it seems to be so frequent in the case of ducks of various species that for them it can scarcely be called abnormal. The peculiarity of abmigration lies in the fact that it is a spring movement by a bird which has performed no autumn movement at all, but has passed the winter in its native area. It is an anomalous spring migration by an individual which one would expect to remain stationary: it is a spring movement which it not the counterpart of any preceding autumn

journey by the bird concerned. It results in a bird native to one area being found in a subsequent summer in quite a different area.

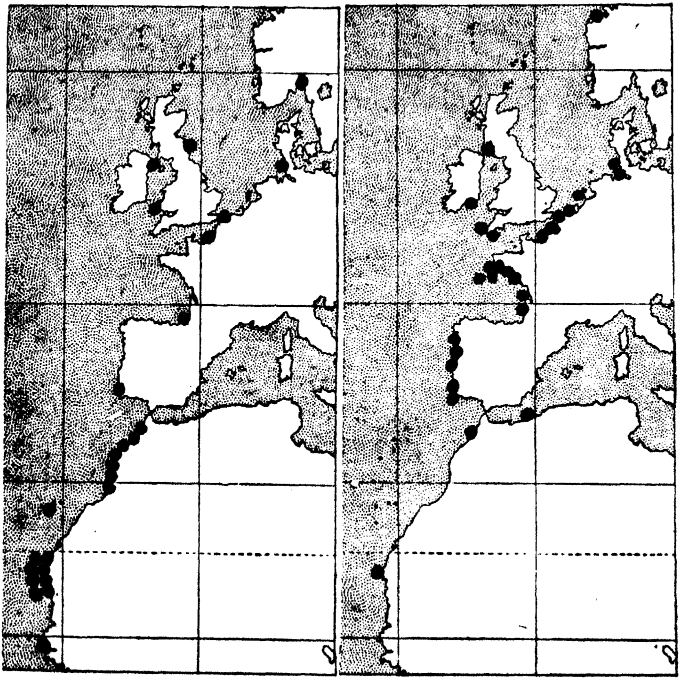
In the case of the mallard there is abundant evidence that in the British Isles the native birds remain practically stationary in winter: although the species has been ringed in large numbers, there are few records showing even movement within the country. Nevertheless, there are a good many records of British native mallard being recovered in northern Europe in subsequent summers. An early instance was that of a mallard ringed in Aberdeenshire as a young bird in the summer of 1910, and recovered in Denmark as a female with a brood of ducklings in the summer of 1911. Since then there have been similar records of birds ringed as young in Great Britain and recovered in Sweden in subsequent summers: there are also records of the same kind for other species of duck.

The occurrence of abmigration may be explained on the assumption that the individuals become attached to flocks of winter visitant birds and accompany them on their normal emigration in spring. It is not improbable that the attachment to a flock of different origin may be due to early pairing, say between a native female and a visiting male. This may also account for cases in which birds return to a different summer area after performing a normal migration in autumn.

Differences dependent on Age or Sex

There are certainly some individual differences in migratory behaviour that are a matter of age. In many species the young birds of the year migrate in autumn separately from their parents—a point, already mentioned, which it is important to note for

other reasons. There is no general rule as to the order, and in many cases the movements of old and young intermingle or overlap. In some instances the first movement is that of young birds, often while it



(a) First year birds. (b) All older birds.

FIG. 11.—WINTER RECOVERIES OF GANNETS RINGED AT BREEDING-STATIONS IN GREAT BRITAIN

Each black spot shows the locality of recovery, between November and February inclusive, of a gannet ringed (usually as a nestling) in Great Britain. The southward movement appears to be more pronounced during the first year of life than subsequently, the proportion of winter records from North African and Tropical waters being considerably higher than for second year or older birds.

is still high summer and the travellers are only a few weeks old. As regards long-distance migrants, it seems to be the adults which commonly go first; possibly all depart about the same time, but the adults are more urgent on the way. We have seen that in the case of the common cuckoo, which undertakes no parental duties, the old birds leave northern Europe in July while many of the young are scarcely able to fly.

There are cases in which the young birds are known to be migratory in higher degree than older birds. This is illustrated by the results of ringing young gannets in the British Isles, analysed by the present writer[1]. The records indicate that the southward movement is more pronounced in the first year of life than subsequently, the proportion of winter recoveries from North African and tropical waters being considerably higher than for second year or older birds.

Another point is that in birds which take two or more years to reach reproductive age, the spring migration of the immature individuals may be incomplete. Some of these may even remain in the winter area throughout the breeding season. This probably accounts, for instance, for the presence of white storks in South Africa at a time of year when they might be expected to be nesting in Europe.

There are some differences due to sex. In many cases, as we have seen, the males reach the breeding area in spring a few days before the females. This is true of various warblers which are summer visitors to the British Isles. Among wintering flocks of different kinds of duck, the proportions of the sexes are found to vary greatly as the season changes, indicating some differentiation in their movements. In some cases, where all the individuals do not

[1] A. L. Thomson (1939). In *British Birds*, Vol. 32, p. 282.

migrate, the tendency may be more strongly marked in one sex than in the other. In Mrs. Nice's community of song-sparrows already mentioned, about half the males were resident but only about a fifth of the females.

Geographical Complexities

All these differences between species, communities and individuals, in one respect or another, add to the complexity of the picture which migration presents at any particular place. A region which serves as a summer area for some birds constitutes the winter area of others. A region which is traversed by some birds in one direction is crossed by others on a different line. According to Dr. Ticehurst[1], the East Siberian race of the willow-warbler is known in winter only from East Africa; while the typical form of Eversmann's warbler has a breeding range extending westwards from Asia to northern Norway, but in winter is not found nearer the latter than Siam: these are two remarkable journeys performed by closely related birds—moreover, they cross each other at right angles.

Migration may not only be simultaneously in progress along divergent or intersecting paths, but even in opposite directions although birds of the same species may be involved! This last phenomenon is, of course, local rather than general, the movements being contrary over only moderate distances. On the coast of East Anglia, for instance, local coasting movements proceeding simultaneously in opposite directions are of frequent occurrence. Northward movement in autumn, running contrary

[1] C. B. Ticehurst (1938). *A Systematic Review of the Genus Phylloscopus*, London.

to the more general trend, probably represents a first stage in the dispersal of immigrants which have arrived from the east.

This phenomenon is so remarkable that it may be useful to cite another example of it from a distant part of the world. Dr. Wetmore[1] describes how, on the eastern coast of the province of Buenos Aires, while living in a lonely herdsman's hut among sand dunes far from other habitation, he witnessed an interesting case of opposite lines of migration. "Apparently many shore-birds drive down the broad interior basin of the Rio Paraguay and continue straight south in their rapid flight, until they reach the coast in the vicinity of Bahia Blanca. Here some remain, some pass on south, and a certain number swing around to follow east and then north along the coast to wintering grounds near the mouth of the Rio de la Plata. At the camp mentioned I noted those birds driving by towards the north, while at the same time little bands of sanderlings, occasional knots, and a steady stream of jaegers came directly south by the coastal route. Thus I had spread before me the spectacle of two lines of migration flight, both emanating originally from the same northern sources, but here, near the end of their long journeys, meeting and passing in directions diametrically opposite—one of the most interesting sights that has come to my attention during long years spent in field observation."

Another curious complexity is the presence in autumn of young birds in regions north of the breeding range, as we have mentioned in another connection. This has been noted with regard to various species of herons, especially in North America but also to some extent in Europe, as well as in some other birds. In the late summer the young

[1] A. Wetmore (1926). *Op. cit.*

of the year range for a time some distance beyond the northern limit of the breeding distribution of the species. The results of marking have shown that this is an even commoner occurrence than was formerly evident from purely distributional evidence. They indicate, moreover, that it is not merely a matter of a dispersal in all directions including north, but one in which north is the most favoured direction: this has been brought out in the case of the black-crowned night heron in North America. The European form of this same species has been ringed in some numbers in Hungary and has yielded early records for young birds considerably northward of the native locality: records for later in the season show a southward migration, through Italy and the countries east of the Adriatic Sea, to and across northern Africa.

Seasonal Complexities

Spring movements are not always the counterpart of those observed in autumn. In some cases quite a different route seems to be followed, or the birds pass through or over much more rapidly. The subalpine warbler is abundant in Egypt on spring passage, but unknown in autumn. It migrates from south-eastern Europe and Asia Minor to the western Sahara and Nigeria: in autumn the route presumably keeps north of Egypt. As a general rule autumn migration is the more noticeable: the number of birds is then at its maximum, and the journey seems to be more leisurely and subject to interruption.

We have seen that in the case of the American golden plover the birds migrate in autumn from their breeding grounds on the Arctic tundras south-eastwards to Labrador, and then southwards by Nova Scotia and over a wide stretch of the Atlantic Ocean to the Lesser Antilles and South America.

In spring, however, they return by way of Central America and the Gulf of Mexico, and thence directly northwards through the centre of the United States and Canada.

The complication which results from trans-equatorial migration has already been mentioned. When it is summer in South Africa and the native birds are breeding, there are present in the same area many northern birds for which it represents winter quarters. It is in the southern autumn that they set forth to find the northern spring: at the same time as they depart, other species which have completed their reproduction are also passing north towards winter quarters nearer the Equator. The usual seasonal terminology becomes inadequate when we try to describe the movements of these birds!

We must also notice that not all migration is related to the alternation between summer and winter in the familiar sense. Even among purely tropical birds there is much migration, as has become increasingly recognized in recent years. Here the contrast is between a wet season and a dry season. Of these, the former is commonly the more favourable, and may be regarded as the counterpart of summer: in the period of drought a semi-desert region may become as incapable of supporting bird-life as the frost-bound polar regions.

There are exceptions to this rule, notably among water birds. For many of these the dry season is the more favourable, when the rivers are low and the mudbanks on which the birds feed are consequently exposed. The open-billed stork, which feeds on aquatic molluscs, is thus found nesting in the southern half of Africa when rivers such as the Zambesi are low, but in the northern dry season it is found as a non-breeder as far as the Upper

Nile. Some species breed both north and south of the Equator, at different times of the year; but the individuals breed only once, and there is thus a diffusion of non-breeding migrants at all seasons.

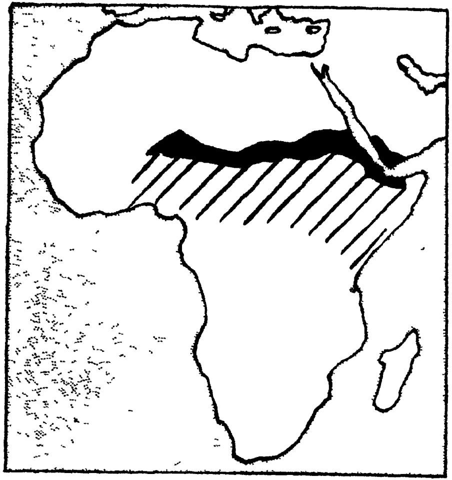
The migrations of various African species of nightjar well illustrate the complexity of the movements taking place within the tropics. The plain nightjar and the standard-winged nightjar both inhabit the region between the Sahara desert and the Congo forest, and are both found in the northern part of this area in the wet season and in the southern part from November or December to June: but the latter breeds in the southern and the former in the northern! Add to this the fact that another species, the pennant-winged nightjar, is found in the same region between March and August as an off-season visitor from its breeding area south of the forest belt. Traversing the region, moreover, are the trans-equatorial migrations of the common nightjar of Europe. Nor does that by any means exhaust the list of members of this group—consisting of related species of similar habits—which perform different movements affecting, in one way and another, this particular part of Africa.

Some curious facts, also, have recently been brought to light about the seasonal distribution of two species native to Palestine. One of these is a sunbird, which breeds in the lower Jordan Valley, about 1,000 feet *below* sea-level. In winter it is common on the coastal plains and in the hills, from sea-level to 2,000 feet above. The other is Tristram's grackle: it also breeds in the great depression round the Dead Sea, and is a winter visitor to the hills. This is a case of vertical migration in what one would naturally regard as the wrong directions, a very hot breeding area being left for a

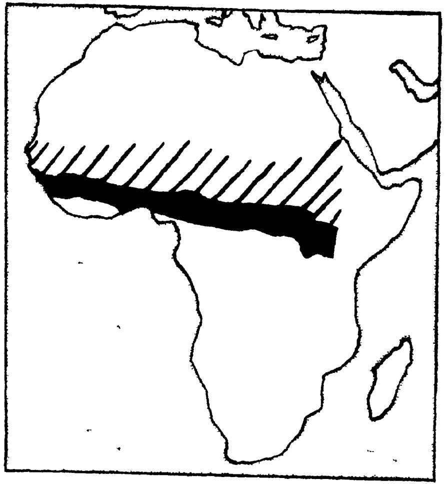
FIG. 12.—SEASONAL DISTRIBUTION OF TWO TROPICAL SPECIES OF NIGHTJAR

After J. P. Chapin

The breeding areas are shown in black and the off-season areas are diagonally shaded. Both species are found in the northern part of their range in the wet season, and in the southern part from November or December to June, but they breed at opposite times.



(a) Plain nightjar.



(b) Standard-winged nightjar.

cold winter area. Moreover, the horizontal movement—of no great length—is mainly northwards in autumn. Reasons for this apparent inversion of normal migratory behaviour are not yet known.

Enough has been said to show that the migration of birds cannot be summed up in any simple formula, but that it includes a great number of phenomena of varied kind, which together make up a picture of much complexity.

CHAPTER IX

THE REGULARITY OF MIGRATION

Recurrent phenomena—Constancy in distribution—Constancy of routes—Accuracy of return—Seasonal regularity.

Recurrent Phenomena

IN spite of their immensity and their complexity, the phenomena of bird-migration are remarkably regular. Comparing one year with another, there is little variation: the movements are repeated, season after season, according to the same general plan. In the main, there is nothing fortuitous about this repetition, and there are only minor differences related to the meteorological peculiarities of the particular year.

It is of course not to be denied that there are many variations in detail. Animal activities are never mechanical in their perfection: one hundred per cent. accuracy cannot be expected. There is always a margin of error, and exceptions are not infrequent.

If we were to concentrate attention on the unusual occurrences in migration, it would indeed be easy to create an impression of great irregularity, but that would be misleading. It is in fact the general regularity of migration that makes the exceptions seem remarkable. Age-long familiarity with the comings and goings of such birds as the swallow has made us take their regularity for granted. It is against that background that the erratic behaviour of a small minority of individuals is conspicuous. It is in comparison with such typical migrants that the less highly developed performances of some other species impress us as being indefinite. The relatively

few which exhibit wholly irregular movements, such as those made at long intervals by Pallas's sand-grouse, are outstanding in a sphere where order and system are characteristic.

Migratory behaviour is constant in the main. Species which are migratory in one year are migratory in others. We have seen that there are differences in behaviour between communities of the same species, but these differences are themselves constant: the Finnish starlings continue to migrate, and the British starlings to remain within their native land. We have also seen that there may be differences between individual members of a single community, some migrating while others remain, but this state of affairs is regular in itself, and is found every year.

With a few exceptions, we thus find that a movement which occurs in one year will occur in another. It will be a movement of the same type on each occasion, whether a mere dispersal or a true migration, and whether it involves a journey of a few thousand miles or only a change in altitude on the mountain sides. The date, the direction, and the extent of the movement will always approximate to a particular standard pattern.

Constancy in Distribution

The foregoing assertions are based upon evidence of a number of different kinds. In the first place there is the constancy which is to be found in the seasonal distribution of different birds. Broadly speaking, the breeding range of a given species remains the same year after year, although it may be largely or wholly vacated during the winter. This fact is of course most noteworthy in those birds which are least widely distributed. In the case of

birds of wide range, however, it is often possible to learn the same lesson from the distribution of the different geographical races which can be recognized within the species. It is indeed reasonable to assume that these races could not have become differentiated unless the communities were segregated from generation to generation: mingling of the stock at the breeding season would tend to prevent the evolution of local types.

Our knowledge of the winter distribution of species is less complete than our knowledge of their breeding ranges: as regards races or sub-species this is even more truly the case. Nevertheless, it is certain that in very many cases the area inhabited in winter is always approximately the same. Very often, too, this winter area is quite small and the annual return to it is therefore striking evidence of the regularity of migration. Various kinds of warbler native to the North American continent are found in winter only on particular islands among the West Indies. Thus, as Dr. Wetmore[1] puts it, "Swainson's warbler retires in winter to the Island of Jamaica, while Bachman's warbler is known at that season only in Cuba. Kirtland's warbler, which nests in a limited area in the state of Michigan, goes south-east to concentrate in the Bahamas."

In describing distribution as constant, we state a general rule and do not ignore the fact that there are exceptions. In the first place, the range of a species may be undergoing gradual expansion or contraction over a long period, as the result of some change in conditions which lessens or intensifies the struggle for existence. This obviously does not affect our present argument. Then we have birds, such as the rosy pastor, which at irregular intervals suddenly

[1] A. Wetmore (1926). *Op. cit.*

and temporarily extend their breeding range far beyond its ordinary limits; and others, such as the waxwing, which every few years perform a winter migration of unusual extent. All we need say of these is that they form a small minority as compared with the species which remain approximately constant in their distribution from year to year.

Individual exceptions are of course common. By this we mean the occasional appearance of a few birds outside the normal range of their species: sometimes there is a large party, as in the case of the flock of lapwings which crossed the Atlantic Ocean in 1927. That rather artificial category, the "British List", includes every species which has been known to reach this country in the natural course, even if only on a single occasion. Many of these must be classed, from our local point of view, as uncommon or rare vagrants. Some of them, however, visit us fairly regularly in small numbers, or are suspected of doing so more often than the few actual records suggest. In these cases, we may regard the British Isles as being on the fringe of the distribution of the species concerned, and the appearance of a few individuals as quite normal. In other cases, the occurrences may be regarded as purely accidental, and as relating to individual birds which have for one reason or another strayed far outside their proper range: they represent the wastage, so to speak, of a process which on the whole works with remarkable accuracy. The same comment applies to odd individuals of familiar species which are recorded unseasonably in a part of the range which is usually deserted at the particular date.

It is because these occurrences are exceptional that they attract special interest, and that their importance may be exaggerated. The rarity is always

apt to secure an undue share of attention, whereas it is the behaviour of the overwhelming majority that is really significant. The fundamental facts are the constancy in the distributon of most species of migratory birds, and the infrequency of any sudden occupation of new regions or desertion of old on a large scale.

Constancy of Routes

The existence of a constant summer range and a constant winter range obviously implies some regularity in the annual movements between one and the other: at least the general trend must necessarily remain the same. This is borne out by direct observational evidence, wherever that is available. In those places where much migration may commonly be seen in actual progress, or where great numbers of birds rest temporarily during their passage, the recurrence of the phenomena becomes well known. Thus, in Mediterranean countries to-day there is a regular industry in capturing quail for the market, out of the vast numbers that pass through at the seasons of migration, "when, as of old in Sinai, multitudes come up in the night and cover the land". Long ago[1] it was written: "And there went forth a wind from the Lord, and brought quails from the sea, and let them fall about the camp, as it were a day's journey on this side, and as it were a day's journey on the other side, round about the camp, and as it were two cubits high upon the face of the earth."

Similarly, one may visit the coast of East Prussia in any autumn with the certainty of seeing the impressive spectacle of the passage of the hooded crows out of north-western Russia, a long column round-

[1] *Numbers*, xi, 31.

ing the south-eastern corner of the Baltic, flock after flock and day after day. In fact, in most places where diurnal movements on a large scale are evident, one may to a great extent count on their recurrence in successive years.

In circumstances which are not so favourable, and in respect of nocturnal movements, regularity is less apparent, because what is seen depends so much on the conditions for observation. One may spend many weeks at a lighthouse without ever being fortunate enough to witness a great concourse of birds at the lantern. This happens, as we have already noted, only in the type of weather which limits visibility and gives the rays a dazzling effect. More commonly the migration passes unimpeded and unseen. In the case of some diurnal movements, too, the migration is noticed only when certain meteorological conditions are effective. Sometimes this is again merely a matter of how the flight is performed, slight variations in this respect making all the difference to the possibilities of observation. Although migrants do not ordinarily fly at great altitudes above the surface of the land or sea, quite a moderate height is sufficient to make invisible or inconspicuous a passage of small birds that is readily apparent under conditions which induce them to keep low. Similarly, a movement which is usually completed before dawn may be so retarded as to become partly diurnal.

Much depends, also, on whether a "rush" is in progress. It often happens that when migration has been held back by unfavourable conditions, a change for the better suddenly releases enormous numbers of birds, giving rise to movements on a gigantic scale, concentrated within a short space of time. On other occasions a movement is spread out more thinly over

a longer period, and is on that account much less noticeable. It is indeed remarkable how inconspicuous a considerable diurnal movement can be, if it consists of small birds passing in parties of no great size and not restricted to any very narrow line of flight.

Nevertheless, the constancy of routes is not absolute. The weather, including particularly the direction of the wind, may affect the course of migration to some extent as well as the conditions of observaton. There is not a great deal of good evidence on the point, but some shifting of lines of flight does occur; the appearance of vagrant individuals outside the usual range of their species is also commonly associated with a strong wind from the appropriate quarter. In an analysis of the 1921 invasion of waxwings, Professor Ritchie[1] has shown that nearly all the waves which reached Great Britain from Scandinavia did so while easterly or south-easterly winds prevailed over the North Sea, suggesting that the unusual appearance of these birds here was due to their being blown off a more normal southerly course —but in drawing general inferences it must be remembered that the movements of this species constitute an erratic phenomenon and not a regular migration of the annually recurring type. What is certain, in general, is that the variations caused by wind are much less than we should find if the direction of migration depended solely on that factor. The effect of wind is a modifying and not a determining influence as a general rule, although exceptionally it may have disastrous results,

We must remember, moreover, that for some birds constancy in the directions of their migration is essential for their survival. This is plainly true of

[1] J. Ritchie (1940). In *Proceedings of the Royal Society of Edinburgh*, vol. 60, p. 299.

birds which are summer visitors to islands such as Iceland or New Zealand, Any erratic behaviour on their part, in this respect, would inevitably lead to a failure to reach the limited breeding area, surrounded by wide seas, and thus to the destruction of the community. In the case of the cuckoos native to New Zealand and wintering in Polynesia, any large scale failure to adhere to the normal pattern of their migration would rapidly lead to the extermination of the species. The same is really true, if less obviously, of all kinds of migrants which run the risk of being carried out to sea or into regions incapable of supporting them. No doubt the many species of land birds which migrate up and down the western seaboard of Europe, for instance, pay toll in the shape of individuals which stray or are driven out over the Atlantic Ocean; but it is clear that the proportion so lost cannot represent an excessive addition to the other causes of mortality, or it would be impossible for migratory species to maintain their numbers.

Further evidence of constancy has been found in the extermination of birds following a particular route: were the movements irregular, the depredations of local gunners could have little effect on the supply of birds in subsequent seasons. As Colonel Meinertzhagen[1] says: "the hosts of shrikes, flycatchers, warblers and cuckoos which used to pass north up the Syrian coast have gone, which would indicate that particular communities of birds use especial migratory routes, and that persistent persecution of that community on that especial route will eventually exterminate that community."

The results of the marking method in recent years have abundantly confirmed the other evidence. We now know that not only birds in the mass but also

[1] R. Meinertzhagen (1935). In *Ibis*, XIII Series, Vol. 5, p. 110.

the individuals show great regularity in their migrations. There are, of course, exceptions in all cases, and in some species these tend to be more numerous than in others; in the ducks generally and in the woodcock, for instance, a good deal of erratic behaviour on the part of individuals seems to be usual.

Another reason, of a theoretical kind, for believing in constancy in the directions of migration, is that the routes followed in many cases seem to be explicable only on historical grounds. By this we mean that the route followed in a particular instance to-day seems to be unnecessarily indirect, or else unusual for the area to which the birds belong, but has some relation to the direction in which the species has expanded its range at a comparatively recent date. It is on these lines, for example, that we may perhaps explain the easterly trend of the migration of birds such as the rustic-bunting in northern Europe, from which the common direction of flight for most species is south-westwards. This is a predominantly Asiatic species which has probably spread westwards; considering that it is a summer visitor in Finland, we might expect it to be more than a casual vagrant to southern parts of Europe.

North America provides a number of examples of eastern species which appear to have expanded their range westwards, especially in the north. Thus, the red-eyed vireo inhabits the eastern United States and in Canada extends right across to the west. The birds from western Canada apparently do not migrate down the Pacific coast or through the western states, where the species does not ordinarily appear at any season; it is therefore presumed that they begin by moving eastwards or south-eastwards, and that this may represent a return to an ancestral path.

Likewise, there are Siberian species which have spread into Alaska, but which, on migration, annually retrace their way over the Bering Sea to go south on the Asiatic side. Yet some of these birds, such as Kennicott's willow-warbler and the Alaskan yellow wagtail, have been established in North America for long enough to have acquired characteristics which make it possible to distinguish them as separate sub-species. It is not intended to suggest, however, that migration routes are incapable of further evolution, and that a new way can never be found from a new region.

Accuracy of Return

It had for long been supposed on general—but often scarcely adequate—grounds, that individual migratory birds returned with great accuracy to the identical localities. There was a small amount of evidence to support this view, such as records of birds distinguishable by some abnormality of plumage or the like. The repeated occupation of a particular nesting site was also sometimes adduced as an argument, but it was one which revealed its weakness when the period extended beyond the span of any bird's lifetime.

More recently, the marking method has brought certainty on this point. There are now very many records of ringed birds such as swallows, which are known to travel to distant winter quarters, returning in subsequent summers to the places where they were marked. In some cases this return has been noted for several years in succession. Incidentally, it has been found that although young swallows return to their native localities they tend to nest at some slight distance from the particular spot, while a bird that has once nested commonly returns again and again

to the identical building. If a look-out for returning birds is too restricted, therefore, it may appear that only adults usually come back, but fortunately there has been enough good observation to show that the inaccuracy in the return on the first occasion is within purely local limits.

Not only are birds able to return to the self-same spot from distant parts of the world, but they commonly do so. Ringing has shown that the exceptions are not at all numerous among the more typical migrants, although some other species are less regular in this respect. Taken all in all, in a high percentage of cases the recoveries in subsequent summers, of birds marked in the breeding season, are within a short radius of the point of origin in the particular instance.

The question of return to the same winter locality was a much more debatable one before the days of ringing. Even now, evidence is not nearly so abundant, for the reason that marking has been done largely in summer and that two winter records for a single individual are seldom obtainable in that event. Systematic trapping in winter has produced many records of return to the same place, but where the birds belong to species represented throughout the year nothing is proved by this means.

Our best information on this point thus comes from North America. Systematic trapping in the southern United States has brought within the scope of this method of inquiry species which are wholly absent from the region in summer. Among these there have been records, in the last few years, of birds returning to the identical locality in subsequent winters, sometimes being caught in the same trap year after year. The white-throated sparrow is a case in point: although the summer range of the species does not

extend south of Massachussetts, ringed individuals have been recorded in successive winters from a particular place in Georgia.

We have thus reason to believe that, among the more typical migrants, return to the winter locality is often as accurate as return to the summer locality. In such cases migration accordingly takes place between two fixed points, and its geographical regularity is placed beyond all question.

Seasonal Regularity

In its seasonal aspects, migration also shows great regularity. The accuracy with which summer visitors make their appearance at a particular place about the same date in different years has long been remarked. "Yea, the stork in the heaven knoweth her appointed times; and the turtle and the crane and the swallow observe the time of their coming." There is some variation, of course, and some species are more regular than others: dates for first arrival in numbers are also more reliable than records of possibly erratic individuals.

The point may be illustrated from the dates of the arrival of the swift in England during the years 1905-13, when special records were kept for the British Ornithologists' Club. The earliest dates in these years were, respectively, 12th, 21st, 23rd, 27th, 19th, 23rd, 25th, 17th, and 14th April. The average of these dates is 20th April, the greatest variations are eight and seven days, and the mean deviation from the average is only four days. The swift is chosen here because of the comparative reliability of first dates as a true record of its movements, odd stragglers being less common in this species than in some others.

There is, in fact, a degree of seasonal regularity

in the manifestations of migration which shows that they are not mainly dependent on the meteorological conditions of the particular year. Variation in the weather may affect the dates of migration to some extent, but they do no more than slightly retard or accelerate the movements of the true migrants. The constancy of migration is inherent, and a high degree of regularity is one of its most characteristic features.

PART IV
THEORIES ABOUT MIGRATION

CHAPTER X

THE UTILITY OF MIGRATION

What object does migration serve?—Avoidance of winter cold—Other climatic factors—Darkness—Scarcity of food The objects of return migration—Avoidance of summer heat —Other climatic factors—Light—Abundance of Food—Availability of nesting sites—General conclusion.

IN successive sections of this book we have dealt with the main facts of bird-migration, treated in broad outline; with particular aspects in more detail—the directions, seasons, and method of migration; and with the general features which convey some impression of the nature of migration—its immensity, complexity, and regularity. In conclusion we may now turn to a more philosophical consideration of migration, having regard to the theoretical problems which the known facts present to our minds. These are problems of purpose, of causation and of means. For the most part, the answers which it is as yet possible to offer are no more than partial or provisional solutions: the subject loses nothing of its interest on that account.

What Object does Migration Serve?

The first problem, and the easiest, is that of the utility of migration: what object does it serve? Although we may well believe that no purpose presents itself to the bird's mind, it is clear that migration must serve useful ends. It must benefit

the species which perform it or they could not survive. So expensive a proceeding, reckoned in output of energy and in loss of life, could be maintained only if it brought some great advantage in the struggle for existence, more than repaying its cost.

It is obvious, up to a point, what this advantage is. Migration allows a bird to exploit the opportunities of two different areas, each at the season when it meets the requirements of the particular species. These areas may be wide, and thus capable of supporting large numbers of individuals; whereas the area that might be suitable for life throughout the year may be relatively small.

It is thus plain that migration is a means by which the bird's life is adapted to climatic conditions, and to the seasonal changes in these. Another factor comes in, however, and that is the seasonal changes in the bird's own needs, as between the period of reproductive activity and the remainder of the year. What we have to deal with is the effect of the interplay of these two series of changes. In its essentials, migration consists of periodical movements between two alternative habitats, one of which is the breeding area and the other is an area of non-reproductive life. As a general rule, the former may be called the summer area and the latter the winter area of the birds concerned.

Part of the answer to our question is, accordingly, that migration provides a useful means of avoiding unfavourable climatic conditions associated with particular seasons in any given area; but, when we look further into the problem, it is not altogether easy to be sure exactly what factors in climatic change are important in this respect.

Avoidance of Winter Cold

The most obvious difference between summer and winter is that of temperature, and this is undoubtedly an important factor in determining the seasonal distribution of birds. Just how important is another matter; and also whether the influence is simple and direct or makes itself felt in some more subtle way. Avoidance of the cold and stormy weather of winter in high latitudes is certainly among the advantages conferred by migration, although it may not have the predominant importance with which we might be inclined to invest it at first sight. It would be easy to show that the extent to which northern lands are deserted in winter depends much more on their climate than on their mere latitude. Moreover, autumnal migration usually takes place towards an area of higher temperature, even where that results in a journey on an east and west rather than a north and south line. On the return journey, also, we have seen that the spread of a species into its breeding area is related to some extent, although seldom exactly, to the advance of spring as shown by the isotherms for different dates.

As to how far temperature is of direct importance for birds, investigations by Dr. Kendeigh[1], in America, have given interesting results. His work, partly experimental and partly based on field data, led him to the conclusion that for every kind of bird there are definite limits of temperature tolerance, beyond which it cannot survive. In his view, the possible range of the species is determined by these limits: the bird can, in fact, exist only within a "zone of physiological comfort", the geographical position of which naturally varies with the time of year.

[1] S. C. Kendeigh (1934). In *Ecological Monographs*, Vol. 4, p. 299.

A point of special interest which emerged from this work was that the lower limit of tolerance is not fixed at any particular temperature level which can be regarded as critical. The matter is more complex than that, because the degree of cold that can be tolerated depends on the length of time during which it must be withstood without replenishment of the body-heat by feeding—in other words, normally on the length of the night. This conclusion is in accord with general physiological principles, and also with previous knowledge as to the very low temperatures which summer visitant species, and even some tropical birds, can tolerate in captivity if adequately fed. Dr. Kendeigh was able to show, however, that in a particular case—the eastern race of the house wren—the northern limits of range, in summer and in winter respectively, could be defined by a quantitative factor which combined the actual night temperatures and the length of the nights. Whether a formula of this kind can be applied to the seasonal distribution of many migratory species it remains for further research to show. So far as it may be true, we should expect to see the northern limits depending partly on climate as expressed in minimum temperatures, and partly on latitude.

Other Climatic Influences

Temperature is of course not the only factor in climate. We have mentioned stormy weather, which is specially characteristic of winter in many parts of the world. High winds impede movement, necessitate greater exertion, and decrease comfort. In wintry weather, too, a bird exposed to the wind may become encrusted with ice in a way that is more inimical than mere cold.

(There is also humidity,) which everywhere plays

its part in the general meteorological picture. In the case of tropical migrants it is this factor rather than temperature which we may suppose to be of principal importance. It is rainfall which marks the seasonal changes to which the movements of these birds are related, the alternation being between a wet season and a dry season. Of these, the latter is the one commonly to be avoided, and is in some regions characterized by desert conditions due to the complete drought. In less extreme cases the dry season is not unfavourable for some species: we have seen that it is indeed best for aquatic birds which find their food on the mudbanks when the great rivers are low.

Darkness

The variation in the length of the day provides another important difference between summer and winter, and one which of course depends entirely on latitude. Avoidance of the long hours of darkness in high latitudes, and in the extreme case the perpetual night of the polar winter, may thus be reckoned as another advantage gained by migration.

Here one may feel confident that the importance of the length of daylight is indirect. The short winter's day gives the minimum of time for feeding, and the long night the maximum time for losing body-heat: as we have already seen, the effect of low temperature is enhanced by long hours of darkness.

It may be noted that transequatorial migrants, passing from the temperate zone of one hemisphere to the temperate zone of the other, not only avoid the winter night but enjoy throughout most of the year the positive advantage of the long summer day. On the other hand, birds which migrate entirely within

the tropics always have an equal day and cannot be affected in any way by this factor.

It should be remembered in this regard that many migratory birds are to a greater or less extent nocturnal in their feeding habits. These are not only the primarily nocturnal species such as owls of various kinds, and crepuscular birds such as the nightjar; there are also others, such as ducks and waders, which feed at night as well as by day. In these cases the long darkness cannot by itself be a serious disadvantage, and the effect of low temperatures is at the same time minimized by the continued feeding.

Scarcity of Food

As an alternative to theories which attribute direct importance to climatic factors, we have the view that the influence of these is mainly through their effect upon the food-supply. This effect is twofold. In the first place, birds are dependent for food either on plants or on animals, and among the latter notably on insects. These are themselves greatly influenced by climate and by the seasonal changes therein. Insects, especially, may be abundant in summer and absent in winter. Secondly, even sources of food which remain present during the winter may become inaccessible to birds. Snow buries the food, frost seals it in the ground, and ice covers the water in which it might be sought.

Some general relation between the feeding habits of different birds and the extent to which they migrate is readily apparent. The great development of migration among insectivorous birds is particularly noteworthy. Many of them are outstanding in this respect, both in the distances they travel and in the brevity of their stay in their summer homes: very few of them that are native to temperate latitudes

are non-migratory. Contrast these with the seed-eating birds, of which so many can be classed as "hardy migrants"—remaining much longer in their breeding area and travelling much shorter distances. In the case of aquatic birds and those which probe in the earth for food, the need for leaving regions where water and ground become frozen is quite plain.

It may be remarked, also, that food-supply is a quantitative thing. Particular kinds of food, without disappearing altogether, may become so reduced in amount as to be incapable of supporting large numbers. The migration of some birds of prey is thus made necessary by the migration of so many of their potential victims, although their appropriate food is not wholly absent and their method of obtaining it still remains feasible.

The Objects of Return Migration

So far, we have been considering the matter mainly with regard to the advantages of departure from the breeding area—typically, autumn migration. The second part of the question relates to the advantages gained by return to the breeding area in the following season. If there were no such advantages, one might reasonably expect that birds would obviate the need for migration by becoming permanent inhabitants of what is in fact only their winter area.

The case here is less clear. The difficulty is again to decide what particular factors are important in making the actual summer quarters more suitable as a breeding area. The external factors to be considered are the same as before, but they must be viewed in the light of the special requirements of the season of reproduction.

Avoidance of Summer Heat

Just as avoidance of winter cold is obviously one of the advantages of autumn migration, so may avoidance of summer heat be among those of the return migration in spring. That birds suffer in too hot weather is a fact of observation, and it may be that species native to high latitudes are unable to tolerate the summer climate of regions which they visit in winter. It may be presumed, also, that the young are much more susceptible than the adults: evidence of this is to be found in the care which some parents show in shielding their nestlings from the sun.

Mention has already been made of the work of Dr. Kendeigh, which indicates the importance of temperature in some cases. His findings as to the upper limit of tolerance are rather different from those regarding the lower limit. We have seen that the effect of cold depends on the length of time during which it has to be withstood without feeding. The effect of too high a temperature, on the other hand, is quickly felt. There seems to be, for any species, a critical level of temperature above which the bird is unable to survive for more than a very short while. The limiting factor in this respect, therefore, is the simple one of maximum temperature at the particular time of year.

There are probably many cases in which the advantage of spring migration can be expressed partly in terms of avoidance of summer heat. There are many others where this factor does not seem to have any possible application. There are birds, for example, which spend their winter in regions which may then be as hot as at any time of the year. For them, return migration does not secure avoidance of any temperature higher than they in fact experience:

nevertheless, it does secure this avoidance for the young birds during their period of infancy, and that point may be crucial. In the case of transequatorial migrants, again, the return migration begins during what is autumn in the Southern Hemisphere: they inhabit both their areas during the respective summers.

It is evident, also, that such migrants as those which avoid the severe winter of parts of continental Europe by migrating to the British Isles, return to a hotter summer than is found in the latter. Both they and their young thus become subject to higher temperatures than would be experienced if they remained to breed in the temperate region which serves as winter quarters.

The position is, therefore, that although most birds avoid cold by their autumn migrations, only some avoid heat by their spring migrations. The temperature factor can thus have no more than a limited importance in making return to the breeding area advantageous.

Other Climatic Factors

Nothing more need be said under this head than to repeat that in some cases differences in humidity rather than in temperature mark the seasonal changes to which migration is adapted. In the tropics, departure from the breeding area may have the advantage of avoiding the dry season there: the return movement may similarly avoid the dry season in the alternative habitat. In other instances, as we have seen, it is the wet season which it is advantageous to escape.

Light

Avoidance of the long winter night in high latitudes is an advantage brought by migration: so,

likewise, is enjoyment of the long summer day of those same regions. The benefit of long hours of daylight, as we have seen, is probably the indirect one of giving the maximum period for the collection of food. Clearly, this must have added importance in the breeding season: not only are there other activities, such as nest-building, to consume time and energy, but in many cases the bird has to obtain food not only for itself but also for a sitting mate or for a family of nestlings. In such circumstances no day is likely to be too long.

We have to note once more, however, that there is no advantage in this respect where birds perform their migrations entirely within the tropics; or, elsewhere, on an east and west line without change in latitude. We may also repeat, for the sake of completeness, that the maximum advantage is secured by the transequatorial migrants which spend practically their whole year in the summer of temperate or high latitudes.

Abundance of Food

Not only are longer hours often required by the individual bird for seeking food, but the total quantity of food required is greater in summer. At that time the bird population is at is maximum, and the rapidly growing young often eat enormous quantities. An advantage of return migration is that it makes available at this important period the supplies of food which summer brings in abundance in the breeding area. The tremendous burst of insect life, for instance, which is characteristic of the brief summer of high latitudes, could be but little utilized by birds if there were none there but the few capable of enduring the rigours of the winter climate.

On the other hand, it must be remembered that

many of these birds are quitting winter quarters which appear to have an inexhaustible supply of food throughout the year.

Availability of Nesting Sites

Finally, return migration has the great advantage that it brings the birds back at the appropriate season to an environment which is suited to the breeding requirements of the particular species, and which has room for a large number of individuals. The winter area is often entirely unsuitable in this respect. At the best, there will commonly be only a limited number of nesting sites of any kind, and great competition for them.

It is indeed likely that this factor is of special importance. Birds tend to be exacting in their nesting requirements, although some are notably adaptable, and it is a familiar fact that species which range widely at other times have often a closely restricted distribution during the breeding season.

Animals in general tend to be especially conservative in their reproductive behaviour. A survey of migratory phenomena in different groups shows numerous examples of a dependence on some ancestral breeding environment: there has to be regular return to it for the continuance of the race, in spite of successful exploitation of other habitats for all purposes but this. The generalization holds good for birds, and there is certainly no surer way of exterminating a species than altering the character of its breeding grounds, as by drainage, deforestation or cultivation. The dependence is very striking in the case of some sea-birds, which range widely over the oceans of the world and yet breed only on a few small islands.

General Conclusion

It will be apparent from the foregoing discussion that there is no simple solution even to our first problem, as to what precisely constitutes the utility of migration. There are several possible factors which probably play a part, but none is capable by itself of providing a complete explanation for all cases. The answer may lie in a combination of these factors, and it is likely that their relative importance varies from case to case. Their effects, moreover, may be direct or indirect, acting on the birds themselves or on the food-supply.

The chief advantage of migration is probably that it avoids the risk of starvation which permanent residence in the breeding area would frequently involve, but at the same time enables that area—presumably particularly suitable for the purpose—to be inhabited at the proper season. It seems likely that climatic changes and differences in length of day are important, from this point of view, largely for their effect upon the food-supply of birds and its accessibility.

CHAPTER XI

THE CAUSES OF MIGRATION

The nature of migratory behaviour—Two kinds of causation—The origin of migration—The stimulus to migration—Weather influences—The physiological factor.

WE have seen that migration serves useful ends; and we have discussed the ways in which it is of advantage to the species that perform it. We have now to consider what causes migration to take place. It is essential, for any proper understanding of the problems involved, that these questions should be kept quite distinct: the utility of migration does not explain its cause. An event does not happen simply because it is advantageous that it should.

The Nature of Migratory Behaviour

One hears it said, in an off-hand way, that birds migrate *in order to* escape the cold of winter and the scarcity of food. Such a statement betrays a lack of clear thought. It would seem to mean that the birds deliberately adopt this course of action because they understand what advantages it will bring, just as a human being might decide to seek a milder climate for the winter. This view credits birds with a degree of intelligence which we have no real ground for supposing them to possess; it is, indeed, contrary to all we know about the nature of their minds. The idea also ignores the fact that the hardships and dangers which migration avoids may be unknown to the birds. In the case of long-distance migrants which are absent from high latitudes for half the year, winter is a thing entirely outside

the experience of the race for countless generations.

Or one may hear the alternative proposition that birds are *forced* to migrate by, say, the cold of winter and the scarcity of food. This statement fails to take account of the facts. It may be true to some extent of what we have called the hardy migrants—birds which depart late in the autumn and go no great distance; and the subsequent "weather movements" which some of these exhibit certainly appear to be the direct outcome of severe conditions. The more typical migrants, however, do not wait until conditions become intolerable, but in many cases take their departure long before the approach of winter is apparent. Moreover, the journeys often extend far beyond the range of influences of this kind. The swift, which has usually completely quitted Great Britain before the end of August, cannot be thought of as compelled to leave by the onset of winter. The swallow, which travels from Europe to South Africa, does much more than avoid the rigours of the season in northern temperate latitudes. Or take the case of the orchard oriole in North America, which spends only two and a half months in its breeding area in a region where the summer has none of the brevity that curtails the visits of birds native to the far north. In southern Pennsylvania the orchard oriole arrives about the first week in May and leaves by the middle of July.

The most that can be truly said, on these lines, is that it is *necessary* for birds to migrate. Nature has a purpose, but the birds themselves can be conscious of none. The dangers do not directly compel, but they are instinctively avoided. Migration, then, is a form of instinctive behaviour.

The introduction of this term, of course, does not explain migration, as the nature of instinct is itself

problematical. The term is a convenient one, difficult to replace, but not altogether satisfactory because the idea lacks clear definition. It nevertheless conveys that the mode of behaviour is one for which the capacity is inherited, that it tends to be stereotyped, and that it is a racial rather than an individual characteristic. How it occurs, however, is not a question in any way peculiar to our present subject, and here we can do no more than recognize that what we call instinctive behaviour is an important fact of animal life.

Two Kinds of Causation

In a sense, therefore, we may say that the cause of migration is the existence of the capacity for this form of instinctive behaviour. It is possible, however, to take the question a great deal further than that. This capacity itself must have had an originating cause, which established and developed it in different species of birds. Here we have the problem of the origin and evolution of migration. The capacity for migration, also, must each year be aroused to active expression by some immediate agency. Here we have the problem of the annual stimulus releasing the migratory behaviour. Each of these problems, and especially the second, is worthy of separate consideration in some detail.

Before embarking on this, let us make sure that the distinction between the two kinds of causative factor is clearly understood. One is the remote original cause; the other is the recurring immediate cause. Both are necessary to explain the existence and operation of instinctive behaviour. There are, on the one hand, the factors which have implanted the capacity in the race, and which have shaped its subsequent evolution. There are, on the other hand,

the factors which evoke the active expression of the behaviour at the appropriate times, twice in each year. The contrast is between the hand that packs the explosive charge in the cartridge, and the finger that pulls the trigger to release the latent force.

This analogy will serve to emphasise another important point of principle. It may be asked whether the recurrng stimulus, or "releaser", is in fact very different from an immediate compelling force such as we dismissed from consideration as having no reality. Most certainly it is: assuming the existence of the capacity for instinctive behaviour, the latent energy may be released by an influence too subtle to exert anything but an indirect effect. Given the charge, a touch on the hair-trigger may cause a bullet to travel a mile: without the aid of the dormant power in the explosive, a great exertion of strength would be required to hurl an object even a fraction of that distance. We shall also find, presently, that the stimulus is not necessarily a purely external agency.

Before we go further it will be well to note that the answers to the problems are not necessarily the same for all species of migratory birds. We have already seen that migration may serve different purposes: it is likewise true that it may have originated in different ways, and that it may take place in response to different influences. Indeed, some differences in these respects there must surely be, so various are the circumstances.

The Origin of Migration

Little need be said about the origin of migration, as this is necessarily a matter almost entirely of speculation. In some way this origin is bound up with the evolution of the different species of birds

that exhibit the capacity for such instinctive behaviour at the present time. It may, as one possibility, be assumed that the birds were at first resident throughout the year in whatever area they inhabited. Possibly this was a wide area, under more equable climatic conditions than exist to-day. It may then be supposed that migration was gradually evolved in the face of some slow change in climate which made more and more of the area uninhabitable in winter. An extreme form of this theory invokes the action of a glacial epoch, or ice age, which for the time drove the birds altogether from their original homes; but the suggestion that the species retained through millions of years an urge to return when the ice-cap retreated, and that migration originated in this way, seems far-fetched.

An alternative view is that the original area of resident habitation was relatively small, and that migration evolved as the result of gradual spread into regions suited to the life of the species during only part of the year. It is even possible that migration might arise suddenly, and later become crystallized as a hereditary form of behaviour, through some abrupt effort of range expansion, after the manner of an irruption of Pallas's sandgrouse such as has been described in an earlier chapter.

The two general views are not wholly incompatible, and it is possible to elaborate a theory which assigns a part to climatic change and a part to range expansion. It is also probable, as we have noted, that the origin of migration in different species has not always been the same. In the case of transequatorial migrants, where the two seasonal areas tend to lie far apart, it is likely that the originating factors have been complex, and that in its evolution the present behaviour has passed through various stages.

The Stimulus to Migration

The question of the immediate cause of migration may be more profitably discussed, as it is one on which factual evidence is available and is likely to increase. Given the capacity for migration, developed under the influence of causes operating in the past, what recurrent stimulus or stimuli evoke the behaviour each year, in autumn and spring?

The possible factors are of two kinds, external and internal. We may seek in the environment for influences associated with seasonal change. We may seek in the bird for influences arising from its bodily state, following or preceding the period of reproductive activity. It is practically certain that influences of both kinds are effective; but, in saying this, it must be remembered that the sequence of the seasons and the physiological cycle of the bird's year are in any event closely linked.

We have already remarked, also, that the stimulating influence may be of a subtle kind. A factor which would be quite impotent as a compelling force may suffice to release the power that lies latent in the organism: a gentle touch may awaken the sleeping giant.

Weather Influences

It has been repeatedly shown that certain weather conditions are particularly favourable to the inception of migratory movements. It is, of course, the conditions at the starting point that are effective: there is no mysterious fore-knowledge of the conditions to be encountered on the way or at the destination. Something about these conditions has already been said in an earlier chapter, but we have now to consider them from rather a different point of view.

It is important to notice that the most favourable weather is fine weather, in autumn as well as in spring. The tendency to depart is greatest when the barometer is high, and least when a depression holds sway. (Again we see that the birds are not driven out by adverse conditions.) Anticyclonic weather generally provides good conditions for the journey, often with a favouring wind. Sometimes, of course, very different weather may be encountered at a later stage, possibly with disastrous results.

Temperature also has an influence, depending not so much on whether it is high or low, as on whether it is rising or falling. In autumn, a decline in temperature favours the inception of migration; in spring it is a rise that has this effect. In either case, the influence is greatest when the fall or rise is associated with the high atmospheric pressure which we have already noted as favourable.

Conditions opposite to those just described tend to retard the inception of movements. The most striking results of weather influence are observed when favourable conditions supervene after a period during which migration has been largely held up. It is then that migration becomes noticeable in the form of great "rushes" in which vast myriads of birds simultaneously take part.

Contrary to what one might perhaps expect, wind is not of direct importance in initiating migratory movements. A wind in the right direction does not by itself cause the birds to depart; nor does an opposing wind prevent departure, unless it is very strong. It happens, nevertheless, that the general weather situation which is most favourable to migration frequently also produces a wind in more or less the same direction. In this way, therefore, migration is often associated with favourable winds. At other

times, however, the favourable weather situation is accompanied by an adverse wind, and the movement of birds takes place none the less. A particular migration may be observed, on different occasions, with the wind in every possible quarter.

Migration against quite strong winds, in which the birds can only slowly make headway in relation to the ground, is familiar to observers. There are actually some movements which appear to take place more commonly with a head wind than otherwise, as we have already noticed. Even flight across the sea against a strong wind is not uncommon, although the length and danger of the passage must be greatly increased in these circumstances. The effect of wind on flight, however, is a different question from that of its possible influence on the inception of movements.

A fourth meteorological factor is the degree of humidity. This is not known to have any influence in initiating migratory movements, although Professor Ritchie[1] has suggested that a moist atmosphere may be favourable for breathing without undue loss of the water content of the body, through the lung surfaces, during a long period when it cannot be replenished. When we have more information about migration in the tropics, the degree of humidity may conceivably be found to be effective there as a stimulating factor.

We see, accordingly, that weather conditions play a part in deciding when migration shall begin, and that the important factors in this respect are atmospheric pressure and change in temperature. It is obvious, however, that this is only a partial answer to the question, because the conditions which lead to migration occur from time to time throughout

[1] J. Ritchie (1940). *Loc. cit.*

the year, but are effective in this way only at the proper seasons.

Professor Rowan[1] has given some striking illustrations of this fact as regards Canada. In the case of the mallard, most of the birds leave Alberta in the autumn. Some may linger, however, until the end of November or December; but it is noteworthy that these never go south thereafter, no matter what weather may supervene. They will remain and starve to death after heavy snow has buried their food-supply (fallen grain in the stubble-fields), although they appear to be in good condition and physically fit to fly a few hundred miles to the southward. In one particular year, over two thousand birds on a lake near Edmonton were saved only by being provided with food by Government intervention. In a different year, on the other hand, there was a remarkably sudden, large and early exodus of ducks and geese at the end of October. This was associated with a high barometer and falling temperature—but not reaching any very low figure—and the weather remained fine and mild for some time following.

We may therefore conclude that the weather factor must be merely secondary, producing the particular result only when the birds are in a receptive state—itself the result of some primary factor of a more special kind. This supposition is entirely consistent with the observational evidence. It is well known that, for some time before departure, migrants are commonly in an excited restless state. It is then that we see the "flocking" which birds such as the swallow exhibit. The restlessness may also be observed in captive birds. It is as if a warning signal had been received, and the final order were eagerly awaited. What, then, is the nature of the

[1] W. Rowan (1931). *The Riddle of Migration*, Baltimore; etc.

primary factor which makes birds prepared to migrate as soon as meteorological conditions give the impulse to actual departure?

The Physiological Factor

The primary factor must be something which is peculiar to the special seasons when migration begins: something which is not liable to send our birds journeying southwards in the middle of their breeding season, or northwards while their native land is still in the grip of winter. Two influences which fulfil this requirement have for long been considered possible and may both be involved.

One of these is the decrease in daylight in autumn, and its increase in spring. Assuming that the birds are in some way sensitive to change of this kind, as one can believe, a very attractive explanation is provided. There is no possible factor which could better account for the notable regularity of migration phenomena from year to year: the variations that do occur would be sufficiently explained by the retarding or accelerating effect of the secondary influence of the weather.

The other hypothesis is that the primary factor is physiological, coming from within as the result of changes in the condition of the body. Birds are capable of reproduction only during a definite and limited breeding season occurring once a year, and the beginning and end of this are marked by profound physiological changes. During this period the sex glands are large and active: they influence the functions of the body and the behaviour of the bird in various ways. During the winter these organs are small and quiescent. The presumption is that the state of transition, in spring and in autumn, is one which somehow predisposes the bird to

migration. Considering the immense influence that various glandular secretions are known to have on behaviour, the idea is by no means far-fetched, but we shall see that the relationship may not be so simple.

These two suggestions have both received support, and have also been shown to be connected, by the very interesting work done by Professor Rowan[1] in Alberta. His first experiment was made with slate-coloured juncos; although these are purely summer visitors there, he found that they were able to survive the severe Canadian winter in outdoor aviaries so long as they were well fed and sheltered from the worst of the weather. He found, also, that if they were kept until November—when the sex glands had dwindled to minimum size—they had lost the urge to migrate: on liberation, they showed no inclination to depart. These were the normal birds used as "controls".

In another aviary the juncos were subjected to the influence of electric lamps turned on at dusk, and kept lit for a period which was increased by a few minutes every day. Thus, while the autumn days were naturally shortening, the days in the aviary were apparently lengthening. The result of this treatment was to induce the sex glands of the birds to develop again in the early winter as if it were already spring; this was of course determined on selected specimens killed for dissection. Moreover, when birds were liberated at this stage they left the neighbourhood, unlike the normal control birds, and were therefore thought to have at least attempted migration.

These results provided some ground for believing that the urge to migrate is derived from the sex

[1] W. Rowan (1926, 1929). In *Proceedings of the Boston Society of Natural History*, Vol. 38, p. 147, and Vol. 39, p. 151; etc., etc.

glands in their transitional state—one of regression in autumn and of recrudescence in spring—and that the annual cycle of change in these glands is itself regulated, at least to some extent, by the seasonal shortening or lengthening of the day. Further experiments have since been made, by Professor Rowan himself and by others, which in part confirm the first results and in part introduce various doubts and complexities.

It has been found, for instance, that castrated individuals migrate; and we have in any event to account for the migration of sexually immature birds in the natural state. To meet this apparent objection, Dr. Bissonnette[1] has postulated an inherent rhythm of the pituitary gland controlling the seasonal condition of the sex organs—which is in line with other recent work in endocrinology—and it may be supposed that the state of readiness to migrate depends directly on the pituitary rather than on the sex glands themselves.

In experiments made in California in spring with the Oregon junco, Mr. Wolfson[2] has obtained a result which seems to be at variance with that obtained by Professor Rowan in Alberta in autumn with the related species. Birds wintering in the area were taken into captivity and kept until well after the normal spring migration. They were released in early summer, at a time when they should have been breeding and when their sex glands were in fact fully enlarged. Yet they disappeared until the autumn and had therefore presumably made a belated migration. Marked individuals of a resident sub-species served as "controls", and these continued to be recorded during subsequent trapping and observation in the neighbourhood. The sug-

[1] H. Bissonnette (1937). In *Wilson Bulletin*, vol. 49, p. 262.
[2] A. Wolfson (1940). In *Condor*, vol. 62, p. 93.

gested inference is that "the total physiological and psychological state of the bird is important in inducing its migratory and breeding behaviour, and not the physiological condition of one organ alone"—although some particular organ, such as the pituitary, may sometimes play a dominant part in determining this total state. In the experiment described, the general state of the released birds may have been "sufficiently similar to that state at the normal time of migration to induce migration two months later than usual"; these captives did indeed differ in several respects from wild birds simultaneously on their normal breeding grounds.

It must also be noted that length of daylight cannot be the sole factor regulating the seasonal cycle of physiological states. It cannot operate, for instance, in the case of birds wintering in the tropics, where the days are all equal. A trans-equatorial migrant, moreover, is subject to autumnal conditions at the end of its sojourn in the southern temperate zone, and yet any change in its physiological condition is of the kind appropriate to spring. It remains possible, however, that the reproductive cycle is the important factor in determining the times of migration, so far as adult birds are concerned; and that this cycle is itself regulated by various environmental influences, among which length of day may or may not play a part in any particular case. It is conceivable that the rhythm may be to some extent inherent, and that in a relatively stable environment the periodicity may become manifest with the mere effluxion of time.

We are therefore left with the general impression that there is a primary physiological factor which induces a state of restlessness and of readiness to migrate; and that secondary meteorological factors

then determine the precise day of departure. It may be added that the exact moment of taking flight often depends on the state of the dusk, in the case of nocturnal migrants, but it might be pedantic to describe this as a tertiary factor.

CHAPTER XII

WHAT GUIDES MIGRATION?

General considerations—Visual recognition—Flight without landmarks—"Homing" powers—"Sense of Direction"—The hereditary factor.

THE title of this final chapter has been deliberately given in interrogative form, because it is easier to ask the question than to frame a reply: in the present state of knowledge, nothing approaching a complete answer is possible.

We have seen that there is good reason for the existence of migration; that the instinct to migrate has been developed under the influence of causes operating in the past; and that this finds active expression at the appropriate times in response to seasonal factors of one kind or another. We still have the problem as to how migration is actually performed, with the constancy of direction and destination which are characteristic.

General Considerations

How, in short, do migrants find their way? The problem really goes deeper than that, as we must also ask how they are aware what way they must seek. What is it that decides the path and goal of any particular migration, and how do the birds succeed in following that path to that goal?

There are some things of which we can be certain in negative fashion. Migration, at least in its more highly developed forms, is not haphazard in direction; nor is it merely directed in a vague, general way—towards the south, say, or whatever the favoured quarter may be. Equally is it untrue that

migrants, once they respond to the urge and rise in the air, are the sport of whatever winds may happen to blow. We have seen that migration is too successful in bringing birds to appropriate destinations, and too regular in its manifestations from year to year, to be capable of explanation in any such manner.

The bronze cuckoo is a summer visitor to New Zealand, wintering in the tropical islands lying north-east of Australia. If its southward flight in spring were only vaguely orientated, or were easily liable to diversion by the wind, only a small proportion would hit the mark at all; the majority would pass wide and head for inevitable destruction in Antarctic seas. It is not credible that any species could survive wastage on that scale—a rate of reproduction much higher than is possible in birds would surely be necessary. Even well-directed movements involve a heavy enough loss, through the inevitable toll of the journey, through imperfectly developed powers in some individuals, and occasionally through wholesale disasters due to stormy weather.

We have therefore to assume that a tendency to travel in a particular direction or by a particular route, for a certain distance or until a certain destination is reached, forms part of the inherited capacity for migration. That is not a very satisfactory answer, as it leaves too much unexplained, but we have at least the consolation that the difficulty is of a kind which is encountered in all study of animal behaviour. Accepting this assumption, we are left with the questions—what is the nature of the routes which migrants follow, and by what sensory means are they able to do so?

As regards routes, the answer is twofold. Much migration follows definite geographical features,

such as coast-lines and river valleys. It is not now believed that migration is largely confined to certain main routes of this kind, but it remains true that there is often a great concentration of individual flight-lines where coasts or rivers lead more or less in the right direction.

At other times migration does not appear to be concentrated along particular lines, but to proceed on a broad front across land or sea. In many cases, indeed, there are no obvious geographical features to follow, and in wide sea-crossings there can be none. In these circumstances the birds seem to maintain a direction rather than to follow a route. In an overland passage, nevertheless, the individual flight-lines may possibly be guided by landmarks even although these constitute no obvious geographical feature and although there may be no tendency to concentration.

Visual Recognition

Where migration follows obvious routes, it is safe to say that vision plays a large part in orientation. This is not only the most reasonable assumption, but it is supported by evidence. There is not only a concentration of flight-lines along the course of some geographical features, but migrating birds may often be observed to follow these features with some exactness. Migrants passing along a coast, for instance, may be seen changing the direction of their flight from time to time to conform to some new trend of the shore. The present writer has seen this strikingly exemplified in the case of hooded crows, as already described: successive flocks of these birds, migrating along the Baltic coast, would find themselves flying out to sea at a point where the land bent away from their line of flight, and would

then rectify the error by wheeling slightly to take the new direction.

It has been observed, also, that flocks of chaffinches migrating overland will change their direction to avoid crossing stretches of water. This is all the

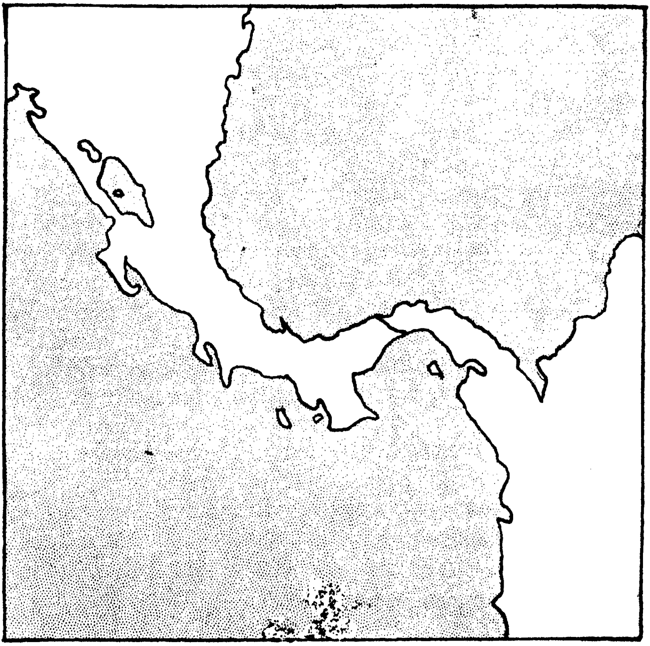


FIG. 13.—ISTHMUS OF PANAMA

Some birds on northward migration fly south or south-west at places on the isthmus, following the trend of the land.

more noticeable when they happen to be flying in a mixed flock with, say, meadow pipits; on reaching the shore of a lake the association breaks up, the birds of the one species changing direction and those of the other holding straight on.

These adjustments of the line of flight to the trend of the land may also take place on a greater scale, involving more than a slight change in direction or a merely local divergence. It has been described, for instance, how large birds of prey may be seen migrating westwards in autumn along the north coast of Asia Minor. When the Bosphorus is reached, they turn left at an angle of more than 90° and continue their journey south-eastwards.

Another instructive case is recorded from Panama. A glance at the map will show that the isthmus has a marked kink, so that, from South America, the land trends north-westwards, then south-westwards, and then north-westwards again: this is responsible for the curious fact that the Atlantic end of the canal is further west than the Pacific end. Following this great bend, the northward passage of turkey buzzards in spring may be seen to double back on itself, so to speak, so that for a while the direction of flight is towards the south or southwest.

In spite of observations such as these, it would undoubtedly be valuable to have more information than we possess at present as to the nature of migration routes, and as to the degree of constancy with which particular paths are followed by particular birds. Especially do we need to know how closely the lines of flight are related throughout to topographical features, and to what extent they are affected by wind and other conditions.

Other evidence showing that vision is important lies in the fact that fog is especially apt to stop migration or to make birds loose their way, although some sea-birds seem to be little affected. It is claimed by some that completely dark nights also hold up migration—moonless nights, with heavily

clouded sky: on less dark nights, coastlines and rivers are likely to be quite visible from above.

Flight without Landmarks

What faculties come into play in the case of migration across the sea is not known. The birds frequently fly only a few feet above the waves, and are then out of sight of land except when quite close to the shore. Even if they flew at great altitudes, their vision could not span many of the stretches of water that are commonly crossed. Yet these crossings are constantly made, in the main with success. Somehow or other the birds seem able to maintain the direction of their flight without the aid of landmarks: whether this is done in relation to the sun and stars, or in some other manner, it is at present impossible to say.

The question is the more difficult because it is necessary to allow for the effect of wind upon flight. When geographical features are being followed, the angle of flight can be adjusted to compensate for the influence of a side wind; migrants can on occasion be observed to resort to repeated "tacking" to regain a line of flight from which they are being blown. Sometimes, of course, a wind of overpowering strength will defeat all efforts, and the birds lose their direction.

Flying without landmarks, however, seems to leave the birds without any means of estimating their lateral drift. They cannot feel the wind, because once they leave the ground they form part of the air-current in which they fly; they move in an apparent calm, feeling no wind except the head-on resistance to their own passage. The case is the same as that of a swimmer in a tidal current, who

cannot judge his real progress except by looking at the shore.

(The suggestion has been made that birds crossing the sea have the power of heading continuously towards a particular unseen point on the other side. On this assumption, it is pointed out, the line of flight would be a long curve—except in a calm or with the wind directly ahead or behind—and the birds would always arrive at the end exactly head to wind. This is what happens to a rower who crosses a river heading always for a point on the other bank, instead of allowing for the current from the outset. There is, however, no evidence at all that birds have this special power, or that they fly in this manner: to assume these things is to beg the question at issue.)

Apart from the question of sea-crossings by land birds, there are the long journeys performed entirely at sea by some oceanic migrants. Examples have been given in an earlier chapter, and in a case such as that of Wilson's petrel the possibilities both of visual recognition and of maintaining an initial direction seem to be irrelevant. Although it is conceivable that the migrations of birds which are at home on the ocean do not demand accurate orientation at all times, it has been proved by ringing that Wilson's petrels commonly return exactly to their particular breeding localities on the Antarctic continent from points which may be as much as 7,000 miles away.

'Homing' Powers

The question of orientation may be approached from another angle by studying the 'homing' powers which are shown by birds. These are certainly remarkable, but one must be cautious about

drawing too close an analogy between feats of homing and the performance of migration; this applies particularly as regards the homing of racing pigeons.

It has to be remembered that racing pigeons are specially bred and carefully trained for the purpose, and that there is an enormous wastage of failures. When young, the birds are trained at first over quite short but gradually increasing distances. As a rule, all these flights are in the same general direction, so that the bird is accustomed stage by stage to the "road" over which it will eventually race.

This statement, however, must be qualified in one important respect. The distances flown are at first increased by easy stages, but later on in the training the jumps are increased. It thus happens that a hundred miles or more of new country has sometimes to be covered before familiar landmarks can be picked up, and how this is done is not understood. Apart from that, flight seems to depend on visual recognition: the birds fly only by day, and the best results are obtained under conditions of good visibility.

Even with careful training, only about five per cent. of the young pigeons survive to race over really long distances, and heavy losses inevitably continue among the experienced birds. A flight of 634 miles in 18¼ hours has been recorded, and greater distances are covered in flights lasting more than a single day. There is, however, a tendency for the time to increase out of all proportion to the distance, and return from a thousand miles away may take many days or even some weeks.

Results obtained in homing experiments with wild birds, removed to a distance from their breeding places, are of more interest. The element of train-

ing over the particular course is here excluded to a large extent, if the flight is in a direction different from that of the presumed normal migration of the birds concerned. In a more general sense, adult birds of migratory species must of course be regarded as experienced.

In 1910 and 1913 Professor Watson and Dr. Lashley[1] of Baltimore, made experiments with noddy terns and sooty terns nesting on the Tortugas Islands in the Gulf of Mexico. Breeding birds taken by ship in closed cages were able to find their way back from distances of over 850 miles, mostly over open sea. Moreover, when removed towards the north the birds were being taken into an unknown region, outside the natural range of their species.

Many other experiments have since been made in different parts of the world with birds of various kinds. Among them are those made by Dr. Rüppell[2] in Germany, with swallows in particular. Swallows taken at their nests and removed by train or aeroplane were shown to be capable of returning fairly quickly, in a good proportion of cases, from distances of 300 or 400 miles. The best time recorded was 255 miles in just under 26 hours.

The present writer was privileged to assist Dr. Rüppell in one experiment, releasing at Croydon one morning in May seven swallows that had been caught near Bremen the previous evening and sent over by air. At least five of these birds successfully made the return journey from near London to their native locality in northern Germany, 428 miles away; the light parts of their plumage had been stained red for purpose of identification, and the first of them

[1] J. B. Watson and K. S. Lashley (1915). *Homing and Related Activities of Birds*, Washington.

[2] W. Rüppell (1934, 1936). In *Vogelzug*, Vol. 5, p. 53; *Journal für Ornithologie*, Vol. 84, p. 180; etc.

re-appeared on the fourth day after release. On a subsequent occasion Dr. Rüppell used house-martins, and some of these successfully made the same return journey.

In further experiments, Dr. Rüppell[1] obtained evidence of successful homing to Berlin on the part of swallows from London, Madrid and Athens; of wrynecks from London, Munich, Venice and Salonika; and of a red-backed shrike from Marseilles. Polish ornithologists[2] have recorded experiments with white storks, in which breeding birds removed from near Lwow returned successfully from Warsaw, from Bucharest, and from Lydda in Palestine—distances of about 185, 410, and 1,400 miles, respectively, the longest journey being made at the rate of 116 miles per day. In the case of these storks, previous migration experience of the country traversed may have helped; but in some of Dr. Rüppell's swallow experiments, for instance, this possibility seems to be excluded.

Remarkable results have been obtained by Mr. Lack and Mr. Lockley[3] in experiments with Manx shearwaters taken from their nesting burrows on Skokholm, off Pembrokeshire. The records include return journeys from Surrey (200 miles in direct line, or 390 miles by sea-route) in 24 hours; from the Firth of Forth (340 miles direct, or 800 by sea) in eleven days; from the Faeroes (730 miles) in twelve days; and from Venice (930 miles direct, 3,700 by sea) in fourteen days. Mr. Griffin[4] has similarly recorded, in experiments with Leach's petrels nesting at the Bay of Fundy, Nova Scotia, a good

[1] W. Rüppell (1937). In *Journal für Ornithologie*, Vol. 85, p. 120.

[2] K. Wodzicki (1938). In *Compte Rendue IXe Congrès Ornithologique International*, Rouen, p. 437.

[3] D. Lack and R. M. Lockley (1938). In *British Birds*, vol. 31, p. 242.

[4] D. R. Griffin (1940). In *Auk*, Vol. 57, p. 61.

proportion of returns from distances up to 470 miles, including returns from points 360 miles from land.

Results of this kind give further evidence of the remarkable powers of orientation possessed by birds, but they do not provide any solution of the problem. One line of explanation is to suppose that, in spite of the conditions of transportation, the birds are able to register the direction of the outward journey, even if it be not in a straight line. To test such ideas, in some of the recent homing experiments with wild birds, the subjects have been transported under an anaesthetic for part of the way, or have been rotated on a gramophone turn-table in the dark throughout the journey, or have been carried in "faradic cages" to exclude possible electrical or magnetic influences. In general, as in earlier work with pigeons, these procedures have not diminished homing capacity in any observable degree.

To sum up, therefore, it is difficult to be certain of anything beyond the fact that birds have a very good visual faculty and a highly developed capacity for topographical recognition. This still leaves much in their powers of orientation to be explained, as they find their way successfully over strange country. Migrants also seem to be able, on occasion, to maintain a general direction of flight in the absence of landmarks, and oceanic birds are necessarily quite independent of these.

"Sense of Direction"

It avails nothing to say that birds must be endowed with a special "sense of direction." To use such a term does not help unless we are prepared to suggest what it means. What kind of bodily function is implied, and with what organ might it be associated? And, again, what is the nature of

the objective factor in direction which is supposed to be perceived in some special way?

The only plausible attempts to give definite shape to the idea of a special sense are based on an assumed sensitivity to the phenomena of terrestrial magnetism. No evidence of any magnetic sense has ever been obtained, however, despite a good deal of experiment. For theoretical reasons, moreover, the suggestion becomes less attractive on examination, because the phenomena seem quite inadequate for the purpose. Ability to perceive the direction of the magnetic pole would not suffice: a compass is of little use without a map, and (in maritime or aerial navigation) without means of estimating lateral drift. If migration took place only along lines having some definite relation to the direction of magnetic north and south, the theory might hold; but we know that migration takes every conceivable direction, and that the stages of a particular journey do not even necessarily continue in the same line.

A more elaborate form of the theory assumes that birds are in some way attuned to the magnetic characteristics of a particular locality, and that when removed from this they can return to it by flying in the direction which increasingly gives them the proper magnetic values. Within certain limits, it is true that every place has its characteristic magnetic "declination" and "dip," and that the same combination of values is found nowhere else. The whole idea as applied to birds is nevertheless purely speculative and open to serious objections. Again we have the absence of any real evidence of sensitivity to magnetic phenomena; and in any event the explanation would cover only "homing" in a more or less straight line, which is a very different thing from many migration journeys.

Admittedly, in ordinary speech we often talk of a person as having a " good sense of direction " (or perhaps " bump of locality "); but by this, however, we merely mean that the individual has his wits about him in the particular respect of finding his way, and that he is observant and has a good conscious or sub-conscious memory for places seen, distances covered, and turns taken. If we stop to think about it, we realise that we have no intention of crediting him with the possession of any special sense unknown to physiology.

A man such as we have indicated will usually excel even on strange ground, without artificial aids, provided that he begins with some general idea as to where his destination lies. Experience has given him a " good eye for country," and has taught him how to pick the best way without deviating unnecessarily from the proper line. It is notorious that individuals differ widely in their powers of orientation; and that members of primitive races greatly surpass, in the main, those of civilized communities. One can readily suppose that animals have still more highly developed faculties of this sort.

The Hereditary Factor

In conclusion, it may be well to recall that in the case of migrants the problem goes still deeper than the question of orientation. It is not merely a matter of finding a way which has been previously traversed by the individual, or of which there is traditional knowledge (such as mankind embodies in a map). When young birds perform their first autumn migration apart from older birds, as many of them do, the way they have to find is one of which they can have no knowledge other than any

which may somehow form part of their inherited urge to perform the journey.

Some attempts have been made to devise experiments to show how young birds migrate if removed, in the egg or before they can fly, to some place distant from their native locality. Results so far have been inconclusive; anything short of a clear preference for some particular direction, reasonably explicable only with reference to the original locality, may mean no more than a failure of the birds to accommodate themselves to abnormal conditions.

A more promising subject than some, for this purpose, is the white stork. We have seen that in eastern Germany the tendency is to fly south-eastwards in autumn towards the Balkan Peninsula, while in western Germany it is to fly south-westwards towards Spain. How, then, will young storks from eastern Germany behave if released in western Germany? Will they be found to have an inherited tendency to fly south-eastwards, or will it prove that there is some factor present in the western area which induces storks to take the south-westerly route irrespective of their origin? A few experiments have been made, care being taken to postpone liberation until a little after all the free birds of the species have left, but the evidence obtained has been conflicting and of doubtful significance. Knowledge of the normal behaviour of storks in western Germany, furthermore, is not yet sufficiently complete to serve as a wholly satisfactory standard of comparison.

Other objections seem to apply in the case of experiments made with mallard caught in winter near the mouth of the Mississippi, the valley of which is regarded as a great central highway for migrating waterfowl in North America. These duck

were released, with rings, at various distant points on the Atlantic and Pacific coasts, and many of them were reported in subsequent seasons back again in the Mississippi Valley. The difficulty here is that journeys from the coasts to the central river are in no way unusual, as the results of marking mallard in the ordinary course have shown; also, the birds were not wholly inexperienced in migration at the time of their release.

Another experiment with mallard is of some interest. Birds of this species native to Great Britain are practically sedentary, as we have noticed before, whereas those in Finland are summer visitors. This suggested the question as to how mallard of British origin would behave if transported to Finland. The matter was put to the test by taking eggs from England and hatching them in Finland. The young were ringed, and the subsequent records showed that they behaved like birds native to the country of their adoption—in the fact of migrating, in the south-westerly direction of doing so, and in return in the following year. This suggests, at least, that British mallard have in no way lost the capacity for migration, although they do not ordinarily travel far. Unfortunately, ducks are by no means typical migrants, but seem especially prone to act in an aberrant manner; individuals are thus apt to accompany other members of their species, as in what we have called "abmigration", in movements which might be supposed to belong to a different inheritance. It is also normal for the young to migrate in flocks with the adult females, and their behaviour may thus be imitative; these birds were artificially reared, but they were released on water where there were plenty of wild birds with which to associate.

What knowledge we have as to the migratory

behaviour of species artificially introduced into new countries does not greatly advance understanding of the problem. No very helpful deductions, for instance, appear to be possible from the case of the European starling in North America, although ringing results indicate that a migration with a fairly definite directional trend has become established. Examples of successful introduction of the long-distance migrants into entirely new regions—say from Europe to New Zealand—are apparently unknown; but, without certainty as to how and why such attempts fail, speculation is useless.

On this aspect of our subject we must perforce end as we began, on a note of interrogation. What determines the direction and destination of migration flight? What enables the migrant to follow that path to that goal? What, in particular, guides the young birds in those cases where they travel apart from their parents when only a few weeks old, and yet perform a long journey in accordance with the constant pattern of their species? Therein lies the real mystery of migration.

"As when a bird hath flown through the air, there is no token of her way to be found, but the light air being beaten by the stroke of her wings, and parted with the violent noise and motion of them, is passed through, and therein afterwards no sign where she went is to be found."—*The Wisdom of Solomon.*

A SHORT LIST OF GENERAL WORKS

In the English Language

(Modern knowledge of bird-migration is contained in a vast literature, to which additions are continually being made. This consists mainly of papers in the orithological journals of different countries, written in many languages. For present purposes, however, it will suffice to refer the reader to a few general accounts of the subject, mostly in book form and all of them in English.)

W. EAGLE CLARKE (1912). *Studies in Bird Migration*: 2 vols. (London & Edinburgh.)

Brings together the results of the author's work, which forms the main foundation of our knowledge of migratory movements in the British area. Includes observations at various island stations, and analyses of the data collected at lighthouses for the British Association.

F. C. LINCOLN (1935). "The Migration of North American Birds." *Circulars of the U.S. Department of Agriculture*, No. 363. (Washington.)

A useful summary account of the main facts and problems of migration, with special reference to North American birds. Replaces an earlier pamphlet by Cooke.

——————— (1939). *The Migration of American Birds*. (New York.)

A popular account for the American reader.

WILLIAM ROWAN (1931). *The Riddle of Migration*. (Baltimore.)

A short general statement, including an account in some detail of the author's important work on the physiological factor in migration.

A. LANDSBOROUGH THOMSON (1926). *Problems of Bird-Migration.* (London and Baltimore.)

A general survey of the subject and a discussion of its problems, with references to earlier literature. Includes a section dealing with the author's work in the analysis of ringing results.

——————— (1929). " Birds, Migration of." In *Encyclopædia Britannica*, 14th Edition, Vol. III. (London and New York.)

A brief summary.

——————— (1936). " Recent Progress in the Study of Bird-Migration : A Review of the Literature, 1926-35." In *Ibis*, XIII Series, Vol. VI, p. 472. (London.)

A supplement to the book of 1926, dealing with the literature of the ensuing ten years.

ALEXANDER WETMORE (1926). *The Migrations of Birds.* (Cambridge, Mass.)

The material of six lectures on various aspects of the subject. Refers especially to American conditions, but also notably rich in examples drawn from the author's wide personal experience in different parts of the world.

H. F. WITHERBY and E. P. LEACH (1931 *et seq.*) " Movements of Ringed Birds from Abroad to the British Islands and from the British Islands Abroad." In *British Birds*, Vol. XXV, p. 110, with subsequent addenda in the same journal. (London.)

These papers usefully bring together the records of marked birds which show movement to or from the British area.

GENERAL SUBJECT INDEX

INDEX OF BIRDS

(It is not considered necessary to encumber the text of a book like this with the scientific names of the species of birds which are mentioned. It is, nevertheless, desirable that these names should be available for reference, seeing that the common names—especially of foreign birds—are not always free from ambiguity. The scientific names are accordingly given in this Index, in parentheses after the corresponding common names.)

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